

Fundamentals of Cognitive Neuroscience

A Beginner's Guide



Bernard J. Baars and Nicole M. Gage



FUNDAMENTALS OF COGNITIVE NEUROSCIENCE

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A BEGINNER'S GUIDE

BERNARD J. BAARS

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Preface

Scientific revolutions are exciting, but they make it hard to keep up. That goes doubly for faculty who want to stay up to date and *also* teach the latest “mind-brain” science to students in psychology, education, economics, political science, sociology, and biology. Popular sources are not always reliable, and specialized journals seem to speak their own languages.

This is our effort to present the fundamentals as clearly and simply as possible. It is based on our upper-division textbook, *Cognition, Brain, and Consciousness: An Introduction to Cognitive Neuroscience*, by Bernard J. Baars and Nicole M. Gage (2010) (Elsevier/Academic Press).

Human beings have thought about the mind and its brain (or vice versa) for many centuries. Scientific psychology emerged from roots in the natural sciences, philosophy, medicine, and the wisdom traditions before 1900. Brain science has its own history. The first accurate anatomy was published by Vesalius in the late Renaissance. Brain anatomy has been studied ever since that time with increasingly fine-grained tools.

Brain functions were much harder to determine—mainly in neurologic patients, followed by postmortem dissection. The living human brain could not be studied directly. That made it hard to find out how the “psyche” and the “brain” relate to each other. The brain is complex and flexible, so it is constantly learning and adapting. Brain damage is not a static thing but a tissue insult that the brain tries to heal, to work around, and to isolate. Postmortem evidence is

therefore important, but it does not necessarily reveal the healthy brain before the injury.

In 1929, Hans Berger was able to detect the tiny (microvolt) electrical field of the human brain for the first time. Berger discovered alpha waves when his subjects were asked to close their eyes. Other basic discoveries followed. Today electroencephalography (EEG) is an indispensable medical tool, but electrically the brain is much like a bowl of gelatin, making it hard to find out *what, where, when, and why*.

Psychological science matured separately from brain science. It was hard to build solid bridges between them. Only in the last decade or so have new and much improved “brain scopes” really taken off. We can now observe the living brain in detail when humans perceive, act, learn, remember, feel, speak, listen, and interact with one another. The effect is much like Galileo’s first view through a telescope: It revolutionized the physics and astronomy of his time. Those sciences used the early telescopes, but they also started to build new and better ones, a process that continues today. The early telescope was still crude, but it had a huge impact.

While our current understanding is far from complete, scientists no longer believe in exploring memory, attention, or the senses from just one point of view. We now want to study those topics from both brain and mind perspectives. The result is not one side “losing” and the other one “winning,” but rather a win-win for both. We are seeing a new synthesis emerging. The whole is greater than, or at least different from, the sum of its parts.

Many practical applications are emerging in medicine, education, and even in the arts. The resulting field is taught under many different course titles. We believe the content is the most important. *Cognitive neuroscience* is our current term of art, but *biopsychology*, *psychophysiology*, and the like can make a claim to the new mind-brain science.

College curricula increasingly demand excellent, up-to-date, and “user-friendly” teaching materials in cognitive neuroscience. The book you now hold in your hands is our attempt to meet that demand. We would be delighted to hear from you and your students.

We have many people to thank for their guidance, assistance, and support throughout the process of preparing this new book. We thank our editor, Mica Haley, for her constant support and guidance throughout this process. Her enthusiasm and friendship were an extra benefit for us! April Graham, our editorial project manager, guided us through the complex and sometimes difficult process of transforming our written words into a printed book, and we thank her for her patience and wisdom during the process. Vanessa McNeill was our godsend during the book preparation. Her organizational and gentle editing truly made the process a pleasure.

Bernard Baars also owes a debt of gratitude to Gerald M. Edelman and many colleagues at the Neurosciences Institute in San Diego for a first-rate education in the

biology of brains—human, virtual, and squid. Nicole Gage wishes to thank Greg Hickok and David Poeppel for their mentoring and friendship as she began her journey to understand the mind and brain.

Most of all, we thank our families and friends for their patience while we created this textbook! Nicole Gage in particular wants to thank her husband Kim for his insight and love.

Bernard J. Baars and Nicole M. Gage

POSTSCRIPT

Our hardcover text, *Cognition, Brain, and Consciousness*, 2nd Edition, has been praised for its accessible approach for students and instructors.

“A powerful pedagogical achievement and a boon for both the novice and the advanced student.”

Patricia Smith Churchland, chair, President’s Professor of Philosophy, University of California, San Diego

“Though intended as a text for students of psychology, biology, education, and medicine, Cognition, Brain, and Consciousness has much to offer the intelligent layperson and even experts in cognitive neuroscience. It’s clearly and entertainingly written, abundantly illustrated, and content rich, making this complex, but fascinating, field accessible to all.”

Stan Franklin, Ph.D., W. Harry Feinstone Professor of Interdisciplinary Research, director, Institute for Intelligent Systems, The University of Memphis, Tennessee

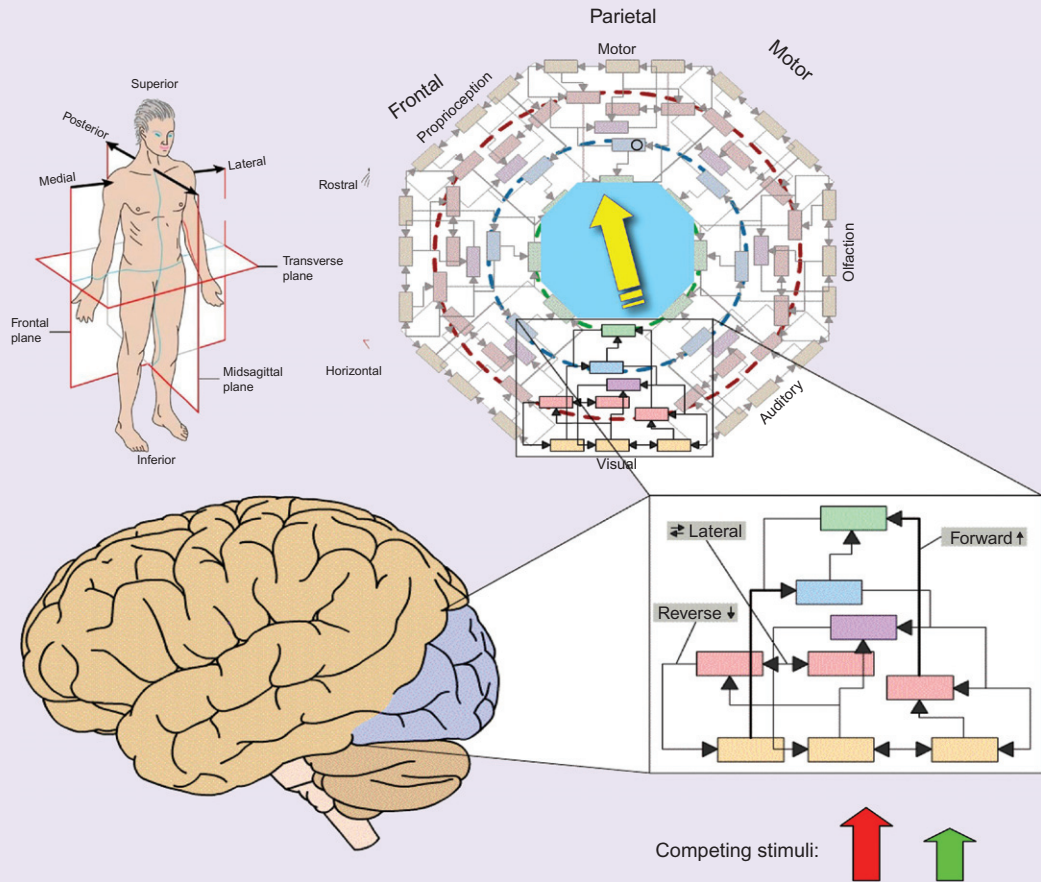
Mind and brain

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LEVELS OF THE NERVOUS SYSTEM

From the brain, and from the brain alone, arise our pleasures, joys, laughter, and jokes, as well as our sorrows, pains, griefs, and tears. Through it, in particular, we think, see, hear, and distinguish the ugly from the beautiful, the bad from the good, the pleasant from the unpleasant. . . . All the time the brain is quiet, a man can think properly. *Attributed to Hippocrates, 5th century BCE (quoted by Kandel et al., 2000.)*



The body has billions of nerve cells, which join into massive nerve tracts to make up the spinal cord and the brain. We can simplify the brain by seeing how its basic units work together.

Source: Drake, et al., 2005

1.0 AN INVITATION

Cognitive neuroscience is the combined study of the mind and the brain. The brain is said to be the most complex structure in the known universe. It can be changed by drinking a cup of coffee or by listening to a favorite song. Some neuronal events happen over a thousandth of a second, while others take decades.

This book is written to simplify the facts. We are in a revolution in our understanding of the human mind and brain. The ability to record from the living brain has brought out new facts, raised new ideas, and stirred new questions. Just ten years ago, we might not have seen a link between cognition and genes, brain molecules, or the mathematics of complex networks. Today, those are hot topics. Some traditional ideas are returning, like consciousness, unconscious beliefs and goals, mental imagery, voluntary control, intuitions, emotions, and the executive self. Many unsolved puzzles remain, but we can see progress.

Brain evidence can help to resolve some long-standing puzzles. In the study of attention, a debate has raged between “early” and “late selection” of attended information. People may pay attention to a coffee cup based on low-level features like color, texture, and location. Or they might focus on the coffee cup based on higher-level properties like “it’s useful for drinking hot liquids.”

Brain studies have shown that attentional selection can affect neurons at almost *any* level. The answer seems to be that there can be *both* early and late selection. In many cases we find good agreement between brain evidence and behavioral evidence.

1.1 Mini-Atlas of the Brain

Please take a look at your Mini-Atlas of the Brain, a foldout from this book. It is a visual guide to brain basics that you can use whenever you need a reminder. Learning the mind-brain takes a little practice. There’s a lot to learn, but we believe it will all make good sense to you.

Notice where the brain is situated in the human head. We normally look at people’s faces, but it takes a little thinking to get used to the fact that our cranium (the bony cradle of the brain) is situated above our nasal cavities and surrounded by a strong helmet of bone, muscle, and other tissues that protect the brain.

The traditional way to learn brain anatomy is to draw brain structures or color existing drawings. Your drawings don’t need to look professional. Just the act of drawing helps. (See the drawing exercise at the end of this chapter.)

Next, the Mini-Atlas shows the three basic “planes of section” that medical anatomists have used for centuries. They are still very useful in modern brain imaging. Notice there is one horizontal plane and two vertical ones. The vertical plane running between the ears is called “coronal” because it looks like a crown. The vertical plane running from the nose to the back of the head is called “medial”.

Over the centuries, when referring to the brain, anatomists used Latin terms for “up,” “down,” “rear,” “front,” “midline,” and “outside.” Latin was the language of science, but complicated words tend to block our understanding of basically simple ideas. Whenever you feel the need, please use the simplest words. For the word “lateral” you might write “(side)” in your notes. “Medial” means “along the midline,” and so on. Keep it as simple as possible.

BOX 1.1

HOW TO LEARN ABOUT THE BRAIN

1. We highly recommend drawing and coloring brain pictures to learn the geography of the brain. As you know, learning requires active involvement. There is no substitute for careful reading, thinking, asking questions, and exploring possible answers. It can be helpful to study with another person. But because the brain is a “hypercomplex surface,” drawing it is especially valuable. This book gives many drawing and coloring exercises.
2. Because the brain is a vast, 3D structure squeezed over millions of years into a very small space, learning it is much like getting to know a city. We can drive or walk around, memorize major landmarks, and visit some of the back alleys and houses. This book will be your guide, pointing out landmarks and the customs of the inhabitants. The more time you spend exploring all its aspects, the sooner you will feel at home with the city map.
3. Each major learning point in the text comes with a demonstration, a figure, or experimental evidence. In the coming chapters we will also see cases of people with brain injuries and explore some of the limits of the normal brain.
4. It’s important to break brain terms into their parts. Anatomical studies began four centuries ago when Latin was the language of science. Many terms are still compounds of Latin. For example, in this chapter we saw the cortex from the side (the lateral view), from the midline (the medial view), the bottom (inferior view), and the top (superior view). Those words—*lateral*, *medial*, *inferior*, and *superior*—have obvious everyday synonyms. Much of our English vocabulary comes from Latin-based languages so you will often be able to spot connections with familiar words.
5. It will help you to do elaborative learning, rather than just repeating new words to yourself. The top of the brain is often called the dorsal part, because *dorsum* means “back” in Latin, and if you look at dogs or cats walking, the top of their brain is an extension of their backs. That is an elaboration of the label “dorsal.”
Elaborative learning is surprisingly effective. If you can turn a technical word into a story or a vivid mental image, it will make learning a lot easier.
Medical students often use memory techniques, such as drawing and coloring. Any kind of active association will help—rhyming, making up visual images, or thinking up analogies. You might visualize the brain as an automobile and associate different structures with the tires or the hood.
6. Don’t worry if your associations seem silly as long as you get a clear mental link between what you are learning and what you already know. Just as there are no bad questions, there are no bad memory techniques—only those that work for you and those that don’t.
7. Finally, self-testing is an essential piece of learning, just as it is for playing guitar. If we don’t test ourselves, we don’t know what we know. Just being able to recognize a word does not mean that you can recall it when you need it. If you expect to pass a recall test, it is important to practice recalling the words on cue. If you study together with a friend, ask each

BOX 1.1 (*cont'd*)

other questions, and you'll see much faster learning.

8. It may help you to browse the web for different ways of looking at experiments and brain images. The National Library of Medicine runs a free web database with tens of millions of scientific abstracts. PubMed will answer all kinds of scientific

and medical questions. There are many outstanding brain anatomy sites and many excellent teaching websites that demonstrate important phenomena for this course.

9. The publisher of this book also maintains a website with brain movies, lecture materials, and PowerPoints.

When you start looking at the inner structures of the brain, remember that the brain evolved over more than 200 million years. Humans share the deeper brain with other animals. For example, the brainstem and hippocampus are major regions in the brains of other mammals as well. In [Chapter 4](#) we “grow” the brain from the bottom up so you can see how the modern brain evolved on top of more ancient structures.

One way to remember the deeper structure of the brain is to keep in mind the lives of other mammals. Infant-mother bonding is a basic mammalian trait, and the neural basis of that behavior is quite ancient. Hunger and thirst, sexual needs, caretaking of infants and children, and interpersonal relationships are represented deep in the brain as well as in the higher levels. These basic life functions are so important that they are spread from the ancestral regions of the brain to the highest levels.

Emotional structures like the amygdala are also “highly conserved” over mammalian evolution. By “highly conserved” we mean that these structures are present in many species of animals. Other mammals show attachment and aggression in ways that resemble humans. However, remember that the gigantic cortex is overlaid on evolutionarily earlier organs. The cortex, especially the frontal lobes, transforms and regulates the brainstem and subcortex.

Finally, in plate 6 of the Mini-Atlas, notice the amazing number of pathways that crisscross the inside of the visible brain. Not only do you have some 100 billion neurons in your brain, but you have even more pathways running among those neurons. The connections are visible to the naked eye as “white matter” because the tiny branches running between cell bodies are covered in white, protective cells. Plate 6 shows the pathways in artificial colors to clarify their spatial layouts. Notice that they travel up, down, forward, backward, left to right, and right to left. At a tinier level, neural signals can even travel through small pathways that we cannot see with the naked eye. Welcome to your brain!

2.0 BASIC CONCEPTS

The human brain is about the size of a small bowl. The sentence you are reading right now will take several seconds to read and understand. Those two features—typical *sizes* and *time intervals*—give us a broad idea of what our range of measurements needs to be. When we look

at the brain in more detail, we can see that there is a huge range of magnitudes in space (distance) and time (or frequency) that we need to consider.

The mind-brain operates over about ten orders of magnitude in distance and about ten orders in time as well. (An *order of magnitude* is a “power of ten.”) Scientists use the metric system, so we will talk in terms 1, 10, 100, . . . (etc.) meters (m), as well as 0.1, 0.01, and 0.001 m.

2.1 Distance: ten orders of magnitude

Figure 1.1 shows some examples for ten orders of spatial magnitude. When we fixate our eyes on a rotating checkerboard checker, the visual part of the cortex becomes very active. Suppose that the rotating disk is ten meters from our eyes in a darkened room, to give a reasonable guess about distance in our normal social world (although we can easily see a

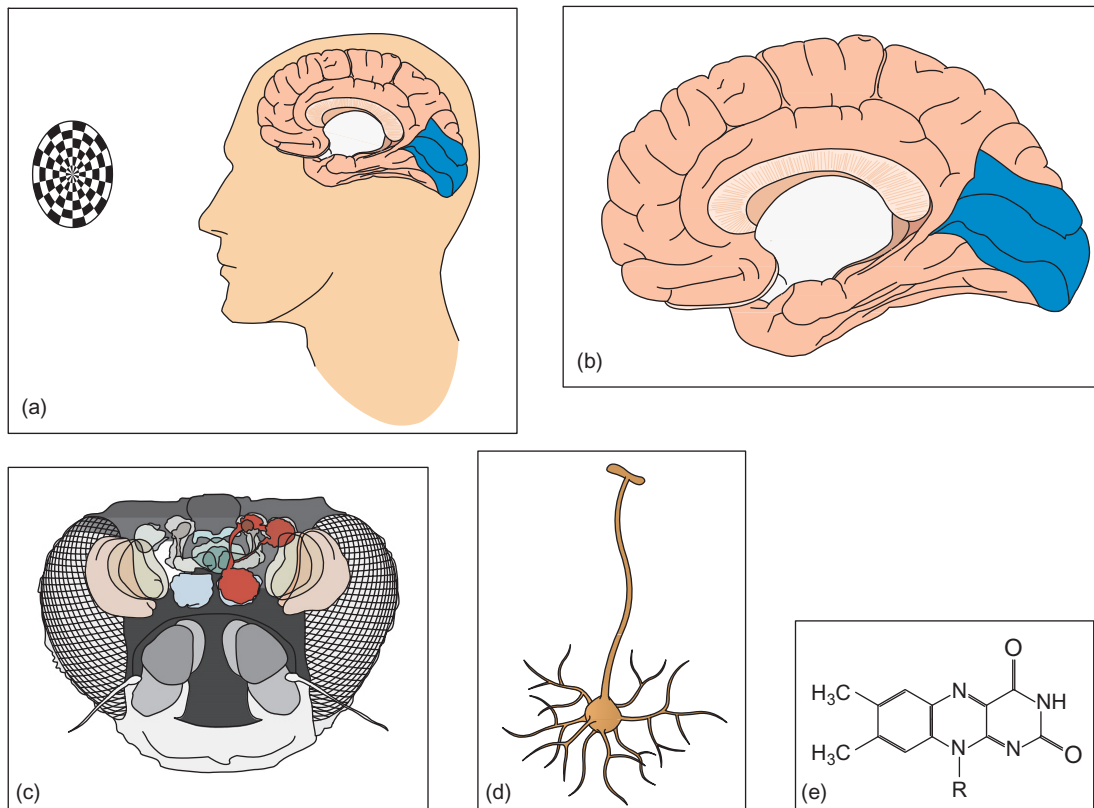


FIGURE 1.1 (a) A brain image of a subject person looking at a rotating checkerboard checker so that the visual cortex (in the back of the brain) is intensely stimulated. (b) A midline view of the cortex, with area V1 marked—the first place where the visual pathway reaches cortex. V1 is about the size of a credit card. (c) The head of a fruit fly. The fruit fly brain has about 100,000 neurons. A single neuron is shown in (d). Neurons vary in size, but they are extraordinarily small; we have tens of billions in our brains. (e) A dopamine molecule. Dopamine plays an essential role in working memory, in the experience of pleasure, and in the control of muscles. Parkinson’s disease is one result of a decline of the dopamine system. From (a) to (e), the range of sizes involves about seven orders of magnitude.

bright star on a dark night). The flashing checker is quickly echoed at the back of the cortex, called area V1, where the optic nerve reaches the cortex for the first time. V1 is the blue area in Figure 1.1(a, b), and it's about the size of a credit card when it is unfolded. V1 corresponds precisely to the retina at the back of your eyes. It has about 140 million neurons.

It's hard to imagine how small a single neuron is. Every cubic millimeter of V1 has about 50,000 cells. The fruit fly in Figure 1.1(c) has about 100,000 neurons, which are remarkably similar to the neurons of other animals. Fruit flies have long been used in biology as “model organisms,” and they have been studied in great detail. Another famous model organism, the tiny roundworm *C. elegans*, has exactly 302 neurons. Nature is full of surprises!

Let's take it down to the caffeine molecules in the coffee you drank this morning. As you probably know from experience, caffeine stimulates your brain. That means a lot of molecules have direct effects on your personal experience, including your ability to stay awake, read, and think. Cognitive neuroscience has to deal with a range from ten meters for our social surroundings to molecules that are around one-thousandth of a micron or one-billionth of a meter. To understand the human mind-brain, we have taken into account phenomena over about ten orders of magnitude. This book will mainly look from the brain to neurons and their signaling molecules. Fortunately, there are many ways to simplify this awesome organ.

2.2 Time: ten orders of magnitude

Human nervous systems operate over a range of time scales and frequencies. “Frequency” is the number of times some event occurs per unit of time. Time intervals and frequencies are two ways of measuring the time domain. Behaviorally, one-tenth of a second (100 milliseconds) is an important time unit to keep in mind. The fastest (“simple”) reaction time to a stimulus is about 0.1 second, and the time it takes for a sensory stimulus to become conscious is typically a few times that. For repetitive events, one-tenth of a second equals 10 Hz (events per second). Two basic brain rhythms run near 10 Hz: the alpha and theta rhythms (Figure 1.2).

One-tenth of a second makes sense in the human environment. If it takes you several seconds to react to an approaching lion or a pack of wild dogs, you would not survive long on the Serengeti Plains. Biologically, you wouldn't get a chance to reproduce. On the other hand, if

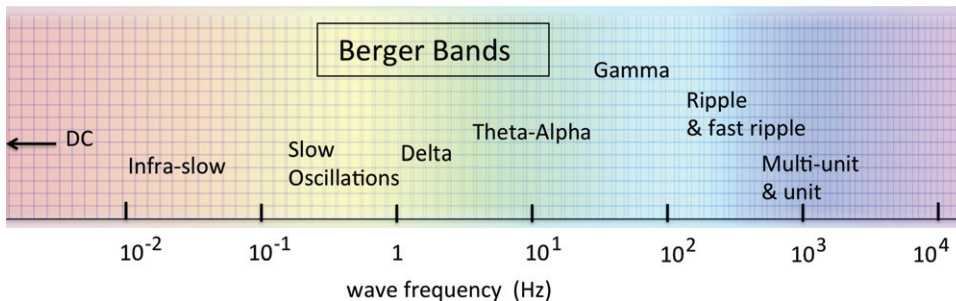


FIGURE 1.2 The frequency spectrum for brain waves and single neurons. Single neurons can fire very fast (see the purple range on the right). Waking activity is in the light blue range, called gamma. When we fall asleep, the dominant brain rhythm slows down to yellow. This diagram does not show days and years because the brain is focused on the here and now. Long-term planning and memory are vital, of course, but they tend to involve *structural brain changes*—the growth of neural connections.

you tried to react as fast as 10 milliseconds—one-hundredth of a second—you would not have time to make intelligent decisions. Sound travels several hundred meters per second, which gives you only 15 seconds to react to that stampeding herd of buffaloes when it's 100 meters away. A meter is about one big step. Therefore, a tenth-of-a-second reaction time gives you some useful middle ground.

Many brain events go on in the same time domain, like the sounds of a song—notes, phrases, and melodies. The smallest time units are combined into larger and larger patterns, like the sounds of language or the notes of a song. When you listen to a song, you are conscious of only a few notes at a time (about a second). Movie frames run at 24 images per second, or about 40 milliseconds per frame, to make them look smooth. At slower rates they start to look jerky and unnatural. These events are in the same approximate time domain. The “present moment” of waking consciousness ranges from 0.1 to 2 seconds, depending on the stimulus. A few words in the sentence you just read would be on the upper end of that time period.

However, the *plot* of a movie takes minutes and hours. In a mystery story, if you can't remember the crime at the beginning, the ending won't make sense. Narratives, like movie plots, play out over minutes and hours. In some cases, like ancient epics and television series, they can take days to go from beginning to end.

The brain needs to make sense of time scales ranging from milliseconds to hours and days. Yet, it can take years to learn a complex skill, like speaking your native language or playing guitar. Infants learn their first language over several years, while adults keep their basic personalities over decades. Such long-term events depend on the same brain as the 100-millisecond reaction time, but they require long-term memory mechanisms, as we will see later. Flexible long-term planning is a human specialty that probably arose with language.

In the time domain, therefore, we also need to understand about ten orders of magnitude, from milliseconds for a single neuron to fire to more than 100,000 seconds in a day and tens of millions of seconds per year. It is again a very wide range of temporal magnitudes.

2.3 Science makes inferences

Science depends on a constant process of inference, going from raw observations to explanatory concepts. Thousands of years ago, when human beings began to wonder about lights in the sky like the sun, the moon, and the stars, they noticed that some were predictable and some were not. The “wanderers” in the night sky were called *planete* by the Greeks, and we call them “planets.” It was not until the seventeenth century that their paths were understood and predicted. The solution to the wandering lights puzzle was to realize that the planets were giant earthlike spheres revolving in orbit around the sun. It took centuries to settle on that solution. Notice that words like “sun,” “planet,” “force,” and “gravity” are *inferred concepts*. They are far removed from the first observations of lights in the sky (Figure 1.3), yet they explain those raw observations.

All science depends on careful observations and conceptual inferences. The resulting explanatory framework has been called a “nomological network”—that is, a network of named concepts and relationships that together provide us a sense of understanding, very much like a semantic network in human psychology. Scientific theories allow us to make predictions

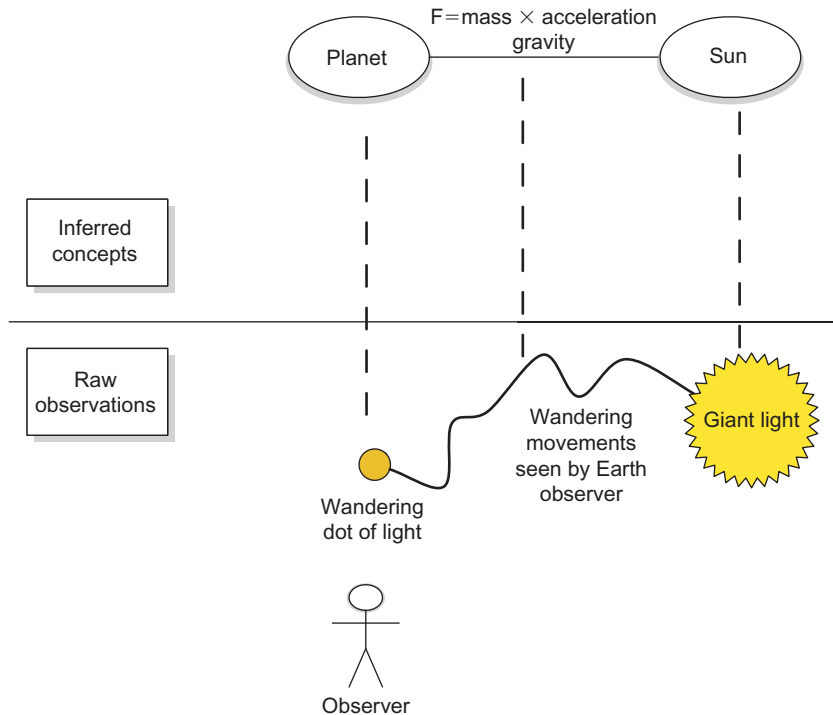


FIGURE 1.3 Inferences about lights in the sky. Humans have watched the planets for tens of thousands of years, noticing that they seem to “wander” around the night sky. It took centuries to understand what the planets actually are and how they orbit around the sun. Science studies raw data to make inferences that may be able to explain the observations.

and to build practical applications. Cognitive neuroscience now has a growing number of applications in medicine, clinical psychology and psychiatry, and even education and economics.

When we talk about human cognition—language, learning, or vision—we also use *inferred concepts*, which must be firmly anchored in reliable observations. For example, the size of immediate memory—the memory items you can mentally rehearse and think about—is about seven plus or minus two items, as George A. Miller famously wrote in a paper called “The Magical Number Seven Plus or Minus Two” (1956). That number seems to apply to many kinds of randomly selected items: colors, numbers, short words, musical notes, steps on a rating scale, and so on. The recent consensus is that the actual capacity of immediate memory is even less than seven—more like about four different items (Cowan, 2001). But the most important point is the remarkable consistency in the data. Try to remember ten different foods on your shopping list, for example, and you will find that only about seven are remembered—and if you are busy thinking about other things, that number drops to four. It is an amazingly narrow limit for a giant brain.

There are only a few basic experimental conditions for finding the size of working memory. Each item must be attended for only a brief time—perhaps several seconds—so that it cannot be

memorized well enough to enter long-term memory. The items must be *unpredictable* from our existing knowledge. If we ask people to recall a regular number series like “0, 5, 10, 15, 20, 25,” they only need to remember the rule, and their working memory capacity will seem endless.

Concepts like “working memory” arise from decades of experiments that finally become so solid that we can summarize them in one basic concept (Figure 1.4). They form a “nomological network” of facts that can be called by a single name, like a city.

Ideas like “working memory” have turned out to be useful, but it is possible that we will find a more attractive way to think about them tomorrow. The facts will not disappear, but we may end up looking at them from a different point of view, just as if a city becomes absorbed in a huge metropolitan area. All scientific concepts are somewhat tentative. Newton’s gravity dominated physics for three centuries, but then Einstein found another way to look at the evidence. Gravity didn’t disappear, but a different point of view gave a larger understanding of the concept. Scientific concepts are always subject to revision.

In cognitive neuroscience we make inferences based on behavioral and brain observations. We don’t *observe* “attention” or “working memory” directly (Figure 1.5). For that reason, it is essential to understand the real-world evidence that we use to make interpretations. Cognitive neuroscience is therefore also based on inferences from raw observations. Because brain scans often look like the brain itself, we are tempted to think that we are seeing “raw reality” in scans. But that is a seductive fallacy. Electroencephalography (EEG) is an *inferential* measurement of brain activity, as is functional magnetic resonance imaging (fMRI), positron

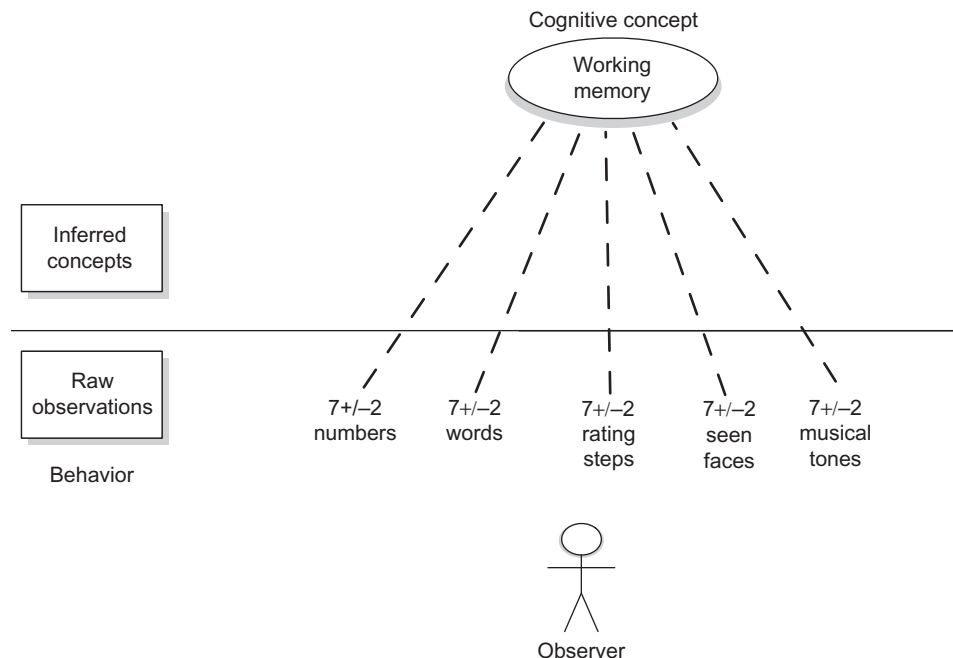


FIGURE 1.4 Cognitive concepts are based on consistent behavioral observations. Concepts like “working memory” are not given in nature. They emerge after many years of testing, when a large body of evidence seems to be explained by an inferred concept. Working memory was proposed in 1974 after two decades of study of immediate memory. Today it has expanded in scope so that visual, verbal, and other temporary buffers are called working memories.

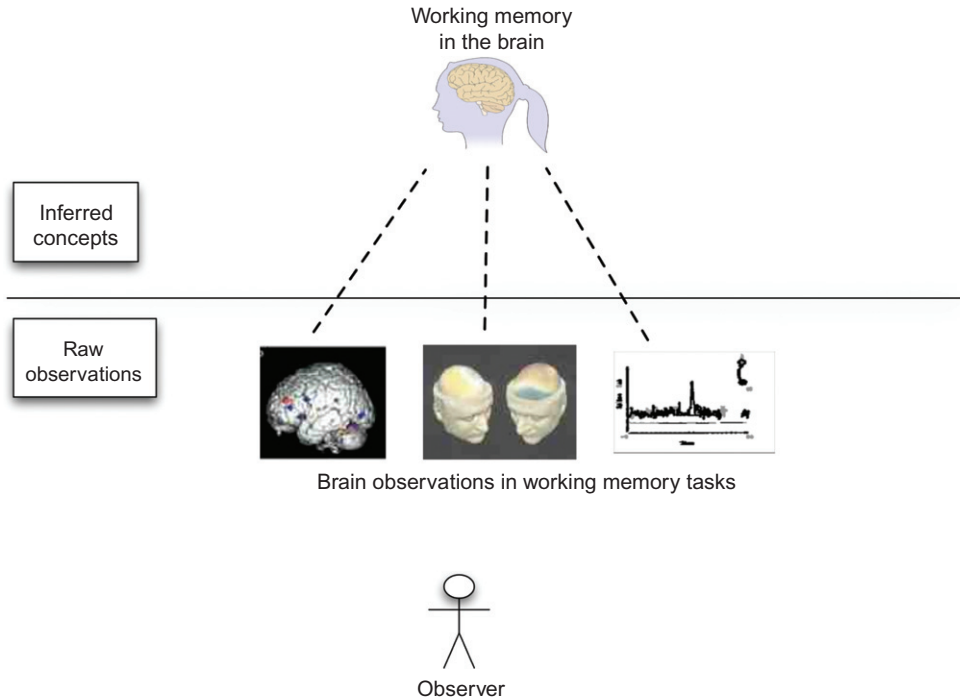


FIGURE 1.5 Brain measures of working memory are also inferential. Working memory functions in the brain have been studied using behavioral measures, but also with fMRI, EEG, and single-neuron recordings. Each of these measures has its pros and cons, but none of them is the “ultimate measure” of working memory. Overall, brain indices of working memory converge well with behavioral measures. Cognitive neuroscience is based on the study of such combined sources of evidence, but we must be prepared to find that our current concepts may be interpreted in a different way.

emission tomography (PET), optical brain recordings, and all the other high-tech tools we have today (see [Chapter 5](#)). Even recording directly from neurons only gives us a tiny sample of the single cell activity among tens of billions of active cells.

Neurons send out thousands of tiny threads that can grow very long. They make perhaps ten thousand connections. There is evidence that even the input branches of a single neuron (the dendrites) may compute information (Alle & Geiger, 2006). Measuring the electrical activity of a single neuron in a single place gives us only a sample of a very complex dance of molecules and electrochemical signals. Brain imaging technology has revolutionized cognitive neuroscience, but it still makes inferences about the working brain.

Yet, we must make *some* simplifying assumptions; that is how science begins. It is important to keep in mind what those assumptions are and to be prepared to change them if necessary. [Figure 1.5](#) illustrates this point.

2.4 Converging measures help to test ideas

When that mythical first cave dweller pointed to a star at night, we can imagine that nobody else in the clan believed him or her. What lights in the sky? The sky was the home of the gods; everybody knew that. That kind of skepticism is the norm. When Galileo first used a

crude telescope to look at the moons of Jupiter, some critics refused to look through the telescope because they believed that only the naked eye could tell the truth.

Skepticism is still the norm, and science always uses *converging measures* to verify observations. Today, any major hypothesis in cognitive neuroscience is tested over and over again, using single-neuron recordings, animal studies, EEG, fMRI, MEG, and behavioral measures such as verbal reports and reaction time. No single study settles a hypothesis. Every major claim requires multiple sources of support.

Part of the debate is always focused on exactly what it is that is being measured. Every new method of observation must answer that kind of question. One popular method today is fMRI. But as we will see, there is ongoing debate about what fMRI actually measures. The same is true of behavioral measures of working memory, single cell recordings, EEG, and all the rest.

2.5 Landmarks of the brain

How does the brain relate to cognition? We present functional brain images to guide you in this text, but brain function is always grounded in the anatomy of the brain. [Figure 1.6](#) (top right) shows the outside view of the left hemisphere, also called the *lateral view*. To the left of the lateral view is the *medial view* of the right hemisphere, also called the *midsagittal section* of the brain. It is a slice that is cut through the midline from the nose to the back of the head. Every other cut that runs parallel to it is called *sagittal* (see [Figure 1.6](#), [1.7](#), and the [Mini-Atlas](#)). We will often put English equivalents in parentheses, so “lateral” (side) or “medial” (midline). Most of the Latin terms have simple English translations.

It’s important to learn the landmarks of the brain. Some of them are big hills or valleys in the cortex—the outer “tree bark” of the brain. The longest valley runs along the midline, straight between the right and left hemispheres, and is called the *longitudinal fissure*. A second large valley flows out at an angle from the side of the brain and is called the *lateral sulcus* (from the word for “ditch” or “furrow”). The lateral sulcus divides the “arm” of the temporal lobe from the “body” of the cortex. Since the temporal lobe always “points” toward the front, it’s the easiest landmark to tell which way the brain is facing. Noticing the temporal lobe is one of the first things to do when looking at a brain.

The *corpus callosum*, another major landmark, is a great fiber bridge flowing sideways between the right and left hemispheres. It is visible on the upper portion of [Figure 1.6](#) as a curved cut that begins behind the frontal lobe and loops up and to the back, ending just in front of the cerebellum. When the corpus callosum is cut, it looks white to the naked eye because it consists of white matter (nerve axons covered by white myelin cells, filled with fatlike lipid molecules). The corpus callosum was called the “calloused (or tough) body” because that is how it looked to early anatomists who named these structures. It was discovered early on because it can be exposed by gently pulling apart the two great hemispheres.

A final landmark is the central sulcus (ditch), which divides the rear half of the brain from the front. The posterior cortex is sensory, with visual, spatial, auditory, and body-sense regions, while the frontal lobe involves motor output (muscles) and mental planning. The central sulcus is a clear vertical valley between the input and output areas of the cortex.

Locating these three major valleys is the first step in orienting yourself to the brain. Like a hillside, the cortical lobes flow over the top to the inside of each hemisphere, as we will see.

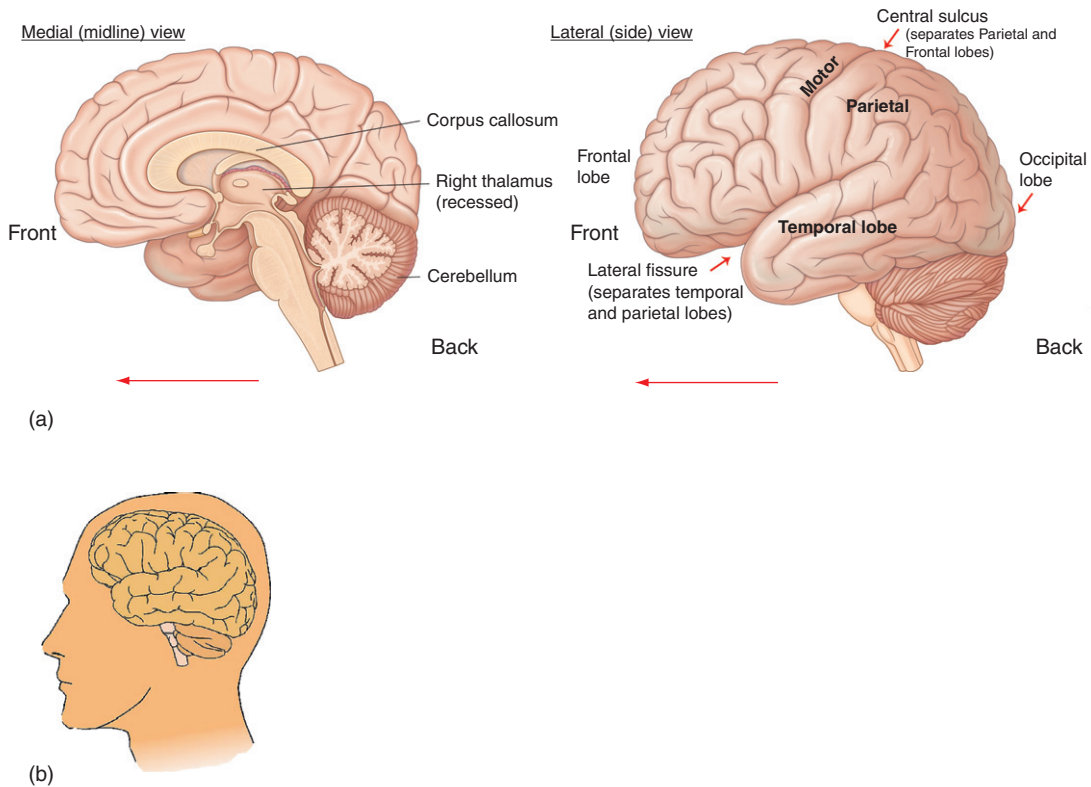


FIGURE 1.6 The brain: midline and side views. (a) The top left panel shows a medial (midline) view of the right hemisphere with major structures highlighted. This view is also called the “midsagittal” slice through the brain. The top right panel shows a view of the left hemisphere from a lateral (i.e., outside) point of view. The front of the brain is on the left, and the back of the brain is on the right. The four lobes of the cortex and the cerebellum are labeled. (b) The lower panel shows a lateral view of the left hemisphere and its location in the head. Source: *Drake et al., 2005*.

Because it’s not easy to understand a knotty 3D object from all perspectives, it will help to hold out your own two fists in front of you to represent the two hemispheres. That makes it easier to keep track of the geography of the brain.

It’s important to know the big lobes and other divisions, just as it’s important to know the continents in geography. Throughout this text we will show brain maps that relate directly to human cognition. The maps will guide our understanding of brain functions throughout this book.

2.5.1 The major planes of section

Medical doctors have studied the brain for centuries. Before computers made it possible to visualize the knotty whorls of the brain in three dimensions, physicians learned about the brain by slicing human and animal brains after death. The simplest approach is to use three major planes of section, meaning straight cuts through brain tissue. [Figure 1.7](#) shows these three major perspectives on the inside of the brain.

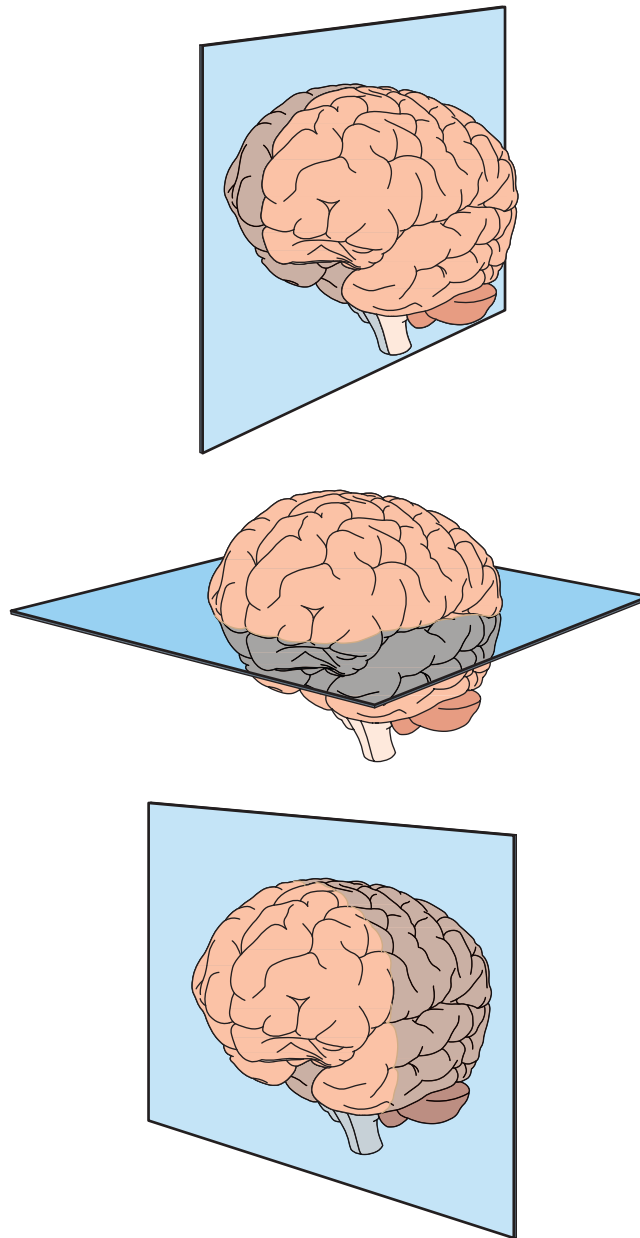


FIGURE 1.7 The three main slices or sections of the brain. The top panel shows a vertical slice, called *sagittal*, from the front of the brain to the back. When the slice is made exactly through the midline, between the two hemispheres, it is called *midsagittal*. The center panel shows a *horizontal* slice through the brain. The lower panel shows a *coronal* section (named for its crownlike shape) like a sliced sausage. Source: Drake et al., 2005.

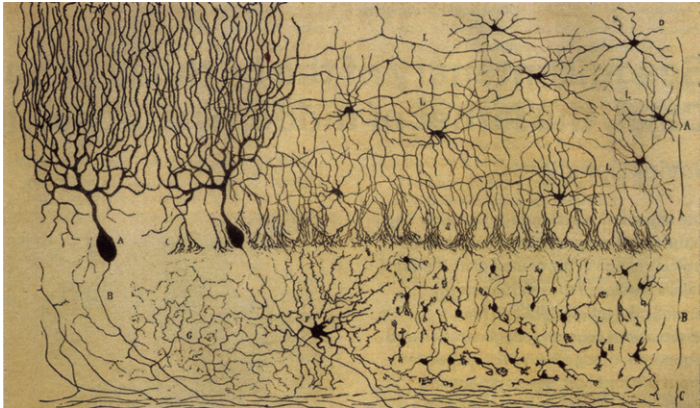


FIGURE 1.8 Cajal neurons. Golgi color stains were used by Santiago Ramon y Cajal, perhaps the most important early pioneer in neuroscience, to bring out basic facts about nerve cells under the light microscope. Cajal showed the microanatomy of neurons. This is his beautiful illustration of his microscopic observations. Source: DeFelipe, 2002.

In medicine and brain science we still look at the inside of the brain using these planes of section, with techniques like MRI (magnetic resonance imaging). Fortunately, we can now do it in living humans and animals without doing any harm.

2.5.2 The nerve cell (neuron)

Many things we think of as obvious today were hotly debated at one time. One of the great debates in early brain science concerned the nerve cell. Without very good microscopes, pioneering biologists were not sure if the brain was made out of separate cells, like other organs, or if the brain might be one gigantic connected network, like the electrical power grid. Ramon y Cajal is remembered today as the microscopist who was able to determine, after many years of painstaking work, that the nervous system is actually made of separate cells (Figure 1.8). This discovery has been so fundamental to neuroscience that Cajal is often considered to be the founder of the brain sciences.

3.0 HOT DEBATES

Today's science is rooted in history. The behavioral sciences date to the nineteenth century, while careful brain studies go back to the very beginnings of modern science in the Renaissance, the time of Galileo, Copernicus, Newton, and Descartes. The perception of pure colors started with Newton's color prism experiments in 1665. The invention of the light microscope by Leeuwenhoek and colleagues in the 1600s led to discoveries of the nerve cell by Santiago Ramon y Cajal three centuries later, around 1900.

The more we learn, the more we can see simple and general patterns in the evidence. We will bring out these simplifying principles throughout. The Renaissance origins of brain science are obvious even today. Brain terminology is often in Latin, the language of science for centuries. We still talk about the *occipital*, *temporal*, *parietal*, and *frontal* lobes of the cortex, all Latin words. Because early studies were done with the naked eye, most anatomical structures were named for the everyday objects they seemed to resemble. Thus, the *thalamus* means the



FIGURE 1.9 Rene Descartes: philosopher, mathematician, brain explorer. Because Descartes was convinced that the soul or psyche was a unified whole, he rejected the idea that paired structures of the brain could support the soul. But almost all of the brain *looks* doubled to the naked eye: two hemispheres, two eyes and ears, two subcortical halves, and two sides of the cerebellum. Descartes therefore decided that the tiny pineal gland, which looks like a tiny dot to the naked eye, must be the point of connection between the divine soul and the earthly body. Unfortunately for Descartes, microscopic studies after the seventeenth century showed that the pineal gland also has bilateral symmetry, just like the rest of the brain. Source: *Bennett, 1999.*

“bridal chamber,” the *amygdala* is the “almond,” *cortex* means “tree bark,” and so on. That fact will simplify your understanding of the labels. We will give the original meaning of each name when it is introduced.

The human brain evolved over some 200 million years from early mammalian origins. It is very complex—even the parts we can see with the naked eye. Centuries of scholarship have contributed to its study. The philosopher Rene Descartes ([Figure 1.9](#)) was a careful student of the brain. In one famous experiment he obtained the eye of an ox; scraped the tissue from the back of the eyeball to expose its tough, white outer shell, the *sclera*; and showed that light images shining through the lens of the eye were projected onto the white sclera like a movie screen. Descartes could see projected visual images by pointing the eyeball at a well-lit object. It amazed many people that the visual stimulus was projected *upside-down* on the back of the eye. Descartes was able to show that this is a direct result of the optics of the lens.

3.1 Mind and brain

Is the world basically mental or physical? Can your conscious experiences be explained by neurons? Maybe nerve cells themselves are just ideas in the minds of scientists. The brain basis of consciousness has now become a mainstream topic again (Edelman, 1989; Koch, 1996; Palmer, 1999; Tulving, 2002; Baars et al., 2003a). In July of 2005, *Science* magazine listed “the

biological basis of consciousness” as one of the top questions for today. Nobel Prize–winning scientists like Francis Crick, Gerald Edelman, and Herbert Simon have devoted years of effort to the question.

In everyday language we switch back and forth between the language of conscious experience and everyday physics. We take a *physical* aspirin for a *mental* headache. We walk to the *physical* refrigerator because we felt a *mental* craving for ice cream. Do conscious experiences “cause” physical actions or vice versa? Common sense doesn’t care. It just jumps back and forth between the language of mind and body. But things get puzzling when we try to think more carefully. In the physical realm of aspirins and refrigerators, ordinary causality explains how things happen. Ice cream melts in the sun, and aspirins dissolve in water. They follow the laws of physics and chemistry. But mental events are affected by *goals, emotions, and thoughts*, which seem to follow different laws. Ice cream does not melt because it *wants* to—but humans eat ice cream because they want to. Human language has thousands of words to describe desires and experiences, but those words don’t apply to physical objects.

For the first time we have a large body of evidence about the conscious brain. Some brain regions, like the “ventral (lower) visual stream,” are believed to support conscious contents, like the sight of a coffee cup. But not all brain regions support conscious, reportable events. For example, the dorsal (upper) visual stream enables hand-eye coordination in reaching for a coffee cup, but by themselves, these areas don’t support the sight of a coffee cup as an object (Goodale et al., 1991). Regions like the cerebellum do not support conscious experiences. The relationship of the conscious mind to the brain is an important, testable question.

3.2 Biology shapes our minds

Human emotions have deep biological roots in the mammalian brain, regulated by more recent layers of the neocortex. The evolutionary history of the human brain, going back two hundred million years to early mammals, is relevant to a host of important questions. Maternal love and infant attachment are rooted in an ancient mammalian brain region called the peri-aqueductal gray matter, or PAG. Sounds of mother-infant soothing and distress seem to have an evolutionary connection to the singsong of language—and maybe even music. Biology turns out to be relevant in many ways.

Charles Darwin helped to establish the biological context of the human species. Darwin made numerous observations about emotional expressions in animals and humans, including his own pets (Figure 1.10). For hundreds of years, people must have noticed the similarities, but in Europe and elsewhere, it was nearly taboo to point out those similarities. There is now good evidence about the emotional brain that we share with other mammals (Panksepp, 2005). In Darwin’s time that idea was very controversial. Today, Darwin’s book *The Expression of Emotions in Animals and Man* is still read as a classic in emotion research (Ekman, 2003).

3.3 Local and global brain activities

How local are brain processes? Do you need your whole brain to learn the material in this course? Or could you just use one part of it? This debate dates back centuries, and it is still going on. Like many enduring questions in science, the answer is that both sides may be right.



FIGURE 1.10 Charles Darwin and the biology of mind. In his book *The Expression of Emotions in Man and Animals*, Charles Darwin cited many examples of human and animal emotions as biologically based. Obviously, culture and individual psychology shape the emotions as well. The picture shows Darwin as a young man, around the time of his historic voyage on *The Beagle*. Source: Finkelstein, 2000.

There are numerous local regions in the cortex, for example, now estimated at about 1,000 specialized patches of the cortex. But like the World Wide Web, the cortex is enormously interactive, with many different areas “talking to” one another. One great challenge in cognitive neuroscience is how to study an organ that is both highly specialized in many locations and also allows for brainwide activities. In the brain, everything is truly connected to everything else.

Suppose part of a long bridge between two parts of a city fell down, as the San Francisco Bay Bridge did after an earthquake ten years ago. How would it affect the people in the city? Some would be personally affected by the damage to the bridge or by the resulting traffic jam. Others would hear about the trouble on the bridge and take a different route, perhaps slowing down their daily commute. Traffic engineers and police would erect stop signs to keep more traffic from taking the blocked bridge and to encourage drivers to take alternative routes. Radio, television, and web services would advise drivers to stay away from the damaged traffic artery.

Telephone and Internet users might not notice any disruption at all, because the physical breakdown of a traffic bridge would not interrupt their lines of communication. The flow of goods, services, and finance to pay for them would not be disrupted. Brain damage is often like that. The brain is a massive “society” of computational networks, and it has many ways of performing its functions. For that reason, when the brain is able to preserve its functions in the face of damage, it often will.

Neurologists have seen this self-healing property of the brain for many years. In the famous case of “split brain operations,” for instance, surgeons cut the corpus callosum in epileptic patients (a relatively easy operation) for decades before scientists like Roger Sperry found that damaging this large bridge between the right and left hemispheres actually created functional impairments. Split-brain patients learned to adapt very quickly to the fact that their right and left hemispheres were no longer talking to each other. They simply moved their eyes from left to right to transfer information that otherwise might travel across the 100 million fibers of the corpus callosum. They learned through trial and error to move their right hands into the left visual field so they could still write and see what they were writing. After recovery from the operation, both doctors and patients were amazed to see how well they could still function after such a large, *local* lesion.

Does the brain work locally or globally? Neurologists who have seen cases of remarkable recovery still debate that issue. Many continue to believe in global brain organization, just as a traffic engineer might have a global perspective on the flow of cars and trucks in the city as a whole. Scientists who study fMRI images of the brain can see local damage, and they can conduct very precise experiments to pinpoint functional impairments. Many brain imagers therefore emphasize a more localist view of the brain.

Both localists and globalists are right. Like a city, the brain is a great collection of local traffic arteries, and they can’t all be stopped without stopping the brain as a whole. But the brain has an amazing capacity to recover from limited damage. Young children below age 6 can even lose an entire language hemisphere after surgery for brain cancer and still recover most of their normal abilities, including speech. Frontal lobotomies were performed 50 years ago for suicidally depressed patients because doctors and patients saw great improvements in the risk of suicide and did not understand the negative effects.

The analogy of the brain to a city is useful because both are designed to work. Both have backup systems to keep running even in the face of serious accidents. Both have multiple communication lines and fuel supplies. Human beings are highly adaptive, even physiologically.

3.4 Conscious experiences are reportable

One of the most mysterious aspects of the brain is that we can *report* some brain activities with amazing accuracy. Some sensory events, like the sight of a single star on a dark night, are extremely tiny, and yet we can report them with very high accuracy. Others, like the sudden tilting of our bodies in an aircraft that is circling for a landing, become conscious only indirectly, since we do not have direct conscious access to the vestibular system that measures the gravitational force on our heads and bodies. We only become conscious of tilt when the whole visual field suddenly seems to move. Other sensory systems, like blood pressure receptors, are entirely unconscious.

Reportability has been used as a “behavioral measure” of conscious experiences for millennia. All human cultures have language, and every language we know allows children and adults to talk about their personal experiences, starting with a baby’s crying when it feels hungry or thirsty. The English language has more than 100,000 words, and more than half of them have to do with our experiences of color, objects, sounds, and other people. Traditional language has a much poorer vocabulary for unconscious brain events, because we can’t talk very much about the things our brains do without consciousness.

Reportability is not the same as conscious experience. People without language (like aphasics who have damage to the language cortex) are often able to signal their experiences by gestures or by pointing to objects. People with hearing impairments can use sign language to convey their experiences in great detail. Language is not the same as consciousness; the brain basis of consciousness is quite different from the basis of language.

Humans are generally unable to report unconscious brain events, even if scientists can observe those events using brain images or behavioral measures. Entire brain regions, like the cerebellum (below the back of the cortex), do not result in direct conscious experiences. But very specific regions of the cortex support very specific aspects of visual consciousness, such as visual color, motion, and even the perception of human faces. People with very local brain damage, for example, are blind to conscious faces. This is called *prosopagnosia*.

Consciousness has therefore emerged again in the sciences as a major, unsolved problem. Nineteenth-century physicians believed that conscious experience depended on the cortex. William James wrote, "The cortex is the sole organ of consciousness in man." Contemporary evidence tends to support James, though some scientists believe that other regions are also involved.

Nineteenth-century scientists were deeply interested in consciousness. One of the founders of brain science, Ramon y Cajal, proposed that there must be "psychic neurons" in the cortex, a specific type of neuron to support conscious experiences. The beginning of psychophysics in the early nineteenth century was inspired by an effort to solve the mind-body puzzle, and the pioneering psychophysicist Gustav Fechner claimed that he had found the answer by showing a mathematical relationship between subjective sensory intensity and physical stimulus intensity. At the end of the nineteenth century, William James proclaimed, "Psychology is the science of mental life," by which he meant conscious mental life (James, 1890/1983, p. 15).

About that time, some began to disagree. Scientists like Helmholtz and Pavlov advocated a more physicalistic view of mental life. After 1900, Pavlov became famous for his experiments on classical conditioning in dogs. This helped to convince many psychologists that ultimately all behavior could be explained in terms of simple behavioral units, like reflexes. In the United States, John B. Watson was the first person to make radical behaviorism famous, arguing that any reference to consciousness was improper, since we can only publicly observe physical behavior and the physical brain. Watson's slogan was that "consciousness is nothing but the soul of theology" and therefore unscientific. For much of the twentieth century, human consciousness was avoided. Some saw it as too burdened with philosophical questions, too difficult to test experimentally, or too subjective to be studied scientifically.

There were some practical reasons for this. It is difficult in many cases to be sure about someone else's experience so it can be hard to repeat experiments in the way reliable science requires. In the 1970s, many psychologists became dissatisfied with behaviorism and began to pursue a different path. While using behavioral measures in the laboratory, cognitive psychologists were interested in making inferences from those observations. We will see one prominent example in this chapter: the idea of working memory. There are many others. Cognitive psychologists have brought back visual imagery, various types of memory, unconscious (implicit) cognition, and many other terms. However, these concepts are always studied behaviorally in the laboratory under very closely controlled conditions. The concepts of working memory, imagery, and so on are inferred from behavioral observations. They are theoretical

explanations, much as electrons are in physics. No one has ever seen an electron, but the concept of an electron explains many different kinds of observable phenomena (Baars, 1986).

Perhaps the greatest change over the last 20 years has been the acceptance of consciousness as a legitimate and workable scientific problem. During much of the twentieth century, the field was tangled in philosophical debates about the body-mind problem or stifled by the limits of introspectionism. More recently, it became clear that neither of these problems represents the sort of fundamental obstacle that was originally feared. Furthermore, the need to account for phenomena such as blindsight and implicit memory, in which perception and recall were clearly proceeding in ways that were at variance with the conscious experience of the perceiver or the rememberer, argued strongly for the need to bring back the study of conscious awareness into the empirical psychological fold. (Baddeley, personal communication).

In recent years, the reluctance to study consciousness has begun to fade. Many cognitive psychologists study both explicit (conscious) and implicit (unconscious) processes. As we will see, there is now a large body of evidence that our perception of the world around us is partly unconscious, although the result of perceptual processing is conscious. Many aspects of memory are unconscious, but recalling yesterday's breakfast makes those unconscious memory traces conscious again. With the advent of brain imaging, it has become possible to make careful comparisons between brain events involving conscious versus unconscious cognition (Table 1.1, Figure 1.11).

Currently, about 5,000 articles per year refer to consciousness and its many synonyms. The synonyms include "awareness," "explicit cognition," "episodic recall," and "focal attention." Those terms are defined experimentally by measures of "accurate report." We simply ask people if they perceived or recalled an event, and then try to check the accuracy of their reports. In that sense, the different synonyms for conscious events are assessed in the same way and therefore seem to have a basic similarity. We will call them "conscious," but we will also use the technical terms (see Baars et al., 2003c).

In the nineteenth century, figures like Sigmund Freud and William James were deeply interested in understanding the relationship between the mind and the brain. Freud began his medical career in neurology and even developed an early neural network model. Early in his career, he discovered a new chemical stain—gold chloride—that allowed certain neurons to stand out clearly under the microscope. The first such stain was discovered by Camillo Golgi in 1873, and it revolutionized the ability to observe nerve cells under the light microscope (see <http://nobelprize.org/medicine/articles/golgi/>).

TABLE 1.1 Conscious and Unconscious Events in Everyday Cognition

Conscious	Unconscious
Explicit cognition	Implicit cognition
Sensory memory	Long-term memory
Attended input	Unattended input
Novel tasks	Automatic habits
Waking and dreaming	Deep sleep, coma, sedation
Declarative memory	Procedural memory

4.0 STUDY QUESTIONS AND DRAWING EXERCISES

4.1 Study questions

1. Name three small-scale spatial events in the brain, with their order of magnitude.
2. Name three small-scale temporal events in the brain, with their order of magnitude.
3. What was the dominant viewpoint about the nature of psychology in the nineteenth century? In the early twentieth century?
4. What is a major difference between behavioral and cognitive psychology?
5. Explain some ways in which psychology and brain science interact.
6. What are some difficulties in studying brain damage scientifically?
7. What is the relationship between the “mental” point of view and “physical” perspective?
8. In everyday life, are you aware of using inner speech? Visual imagery? If so, in what situations? If not, what everyday situations might show that kind of process? (Note that there are considerable individual differences in visual imagery; not everybody reports having spontaneous images.)
9. Which brain landmarks could you use to tell where the eyes are looking?

4.2 Drawing exercise

Here is an easy way to draw the two most popular perspectives on the brain. If you hold up both fists to face each other, you will see that each fist has an “inside” surface and “outside” surface. This corresponds nicely to the two hemispheres of the cerebral cortex.

Looking at your left fist from the left side, you will see the *left side* of your *left fist*. That is the perspective we see in [Figure 1.12](#), this chapter’s brain drawing exercise. If you look at your *right fist* from the surface that faces the left one, you will see the *midline* perspective on your right fist.

Those are the two perspectives on the brain we will draw. If you need to remind yourself of the spatial perspectives, just look at your two fists. Notice that both brain drawings are “looking to the left.” The eyes are therefore on the left side of the page.

We start the drawing by locating the bony ridge above the eyes, which protects the eyes like a pair of motorcycle goggles. That locates your baseline. Draw a horizontal line across your paper or screen. Then construct half a circle on your horizontal line. Notice that the brain (and the cranium, which cradles the brain) is actually more like an oval than a round circle. You now have the red dotted half-circle shown in [Figure 1.12](#).

Now draw in the black outline of the brain itself and the outline of the scalp. A vertical line in the middle of your half-circle will give you a useful guide line for filling in the locations of the two major grooves or folds in this perspective on the brain, called the *lateral fissure* and the *central sulcus*.

Notice that the actual left hemisphere dips below your horizontal line. Be sure to draw in the parts that go below your horizontal guideline. Likewise, the central sulcus swerves across your vertical guideline. The central sulcus is a major landmark of the cortex, because it nicely divides the *posterior cortex* from the *frontal lobe*. The posterior cortex is mostly sensory. The frontal lobe is for motor control and executive functions. Thus the rear half is for analyzing input. The front half is for planning and controlling output. This is a vitally important fact.

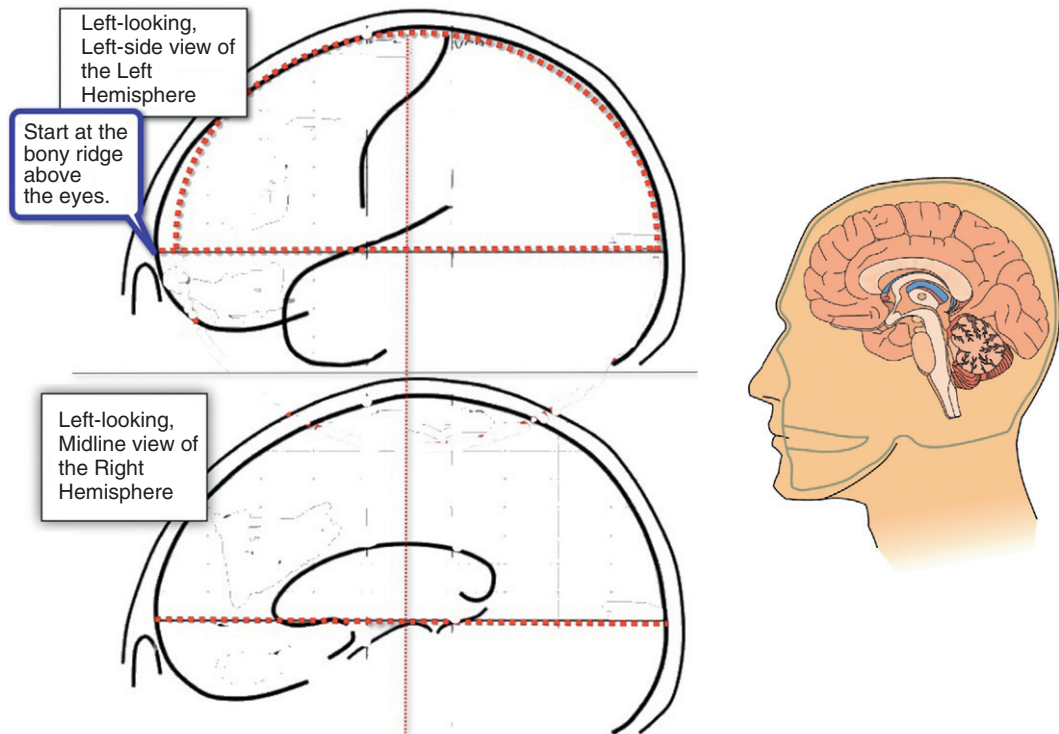


FIGURE 1.12 Drawing exercise.

Repeat the drawing steps with the lower brain figure—the *left viewpoint* on the *midline of the right hemisphere*. Take a look at your two fists if that sounds confusing. You have now drawn your first brain!

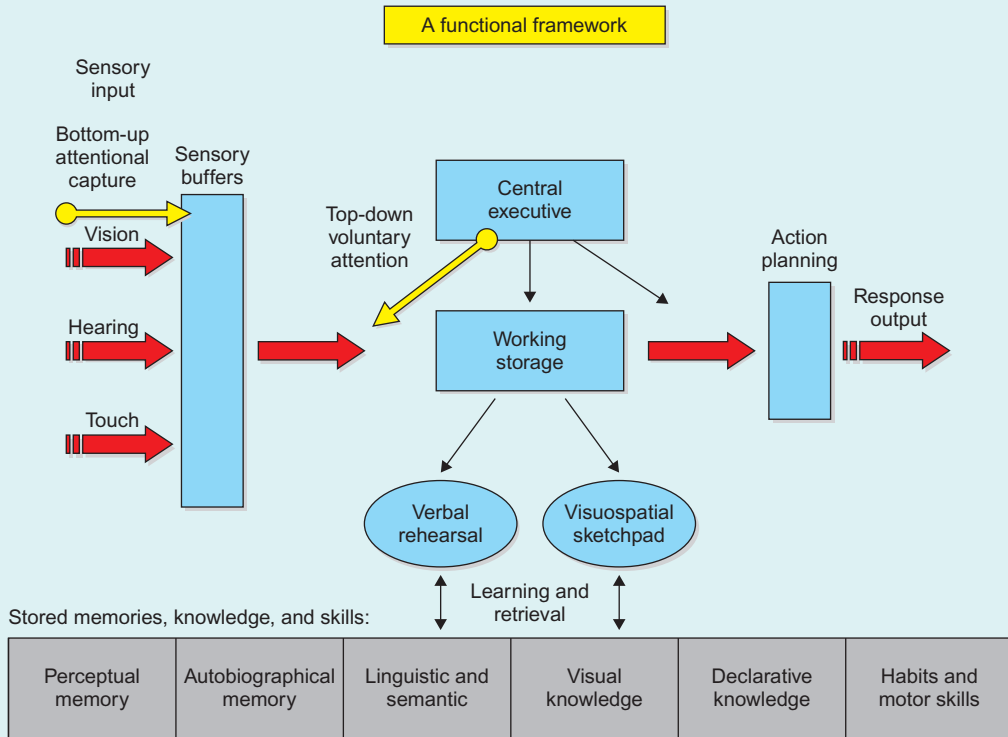
In future chapters you can fill in details in your brain drawing. Drawing is a great way to utilize our spatial brain capacities. Words don't communicate spatial relationships as well as drawings. If you simply draw the main brain regions in this book, you'll find yourself learning much more easily. Drawing in simple guidelines first is a good way to approximate the spatial distances. Your drawings do not have to be perfect. They are for learning.

A useful framework

OUTLINE

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COGNITIVE FUNCTIONS



All the basic functions we discuss in this book can be sketched in this diagram.

1.0 BRAIN REGIONS AND THEIR FUNCTIONS

Here we introduce two diagrams that summarize the book. [Figure 2.1](#) shows *cognitive functions* to help you organize major human abilities like perception, memory, and action. This diagram combines many facts into a single framework, and it will simplify things for you. It is always useful to draw the diagram until you're sure you understand it.

We will briefly touch on each part in the framework shown at the beginning of this chapter and relate it to our second basic diagram, which we call the *cortical functions*. Once you can relate them to each other, you'll know a lot about cognitive neuroscience.

Notice that [Figure 2.1](#) shows only on the cerebral cortex. The left lateral (outside) view is on top, and the medial (inside) view is on the bottom. In later chapters we will describe other brain regions as well. For example, this chapter does not cover the sensory and motor pathways, the great input and output highways of the nervous system. But the cortex is a good place to start because it performs the highest level of analysis for sensory events, and it is also the highest level of planning and control for our actions. The cortex gives us a first

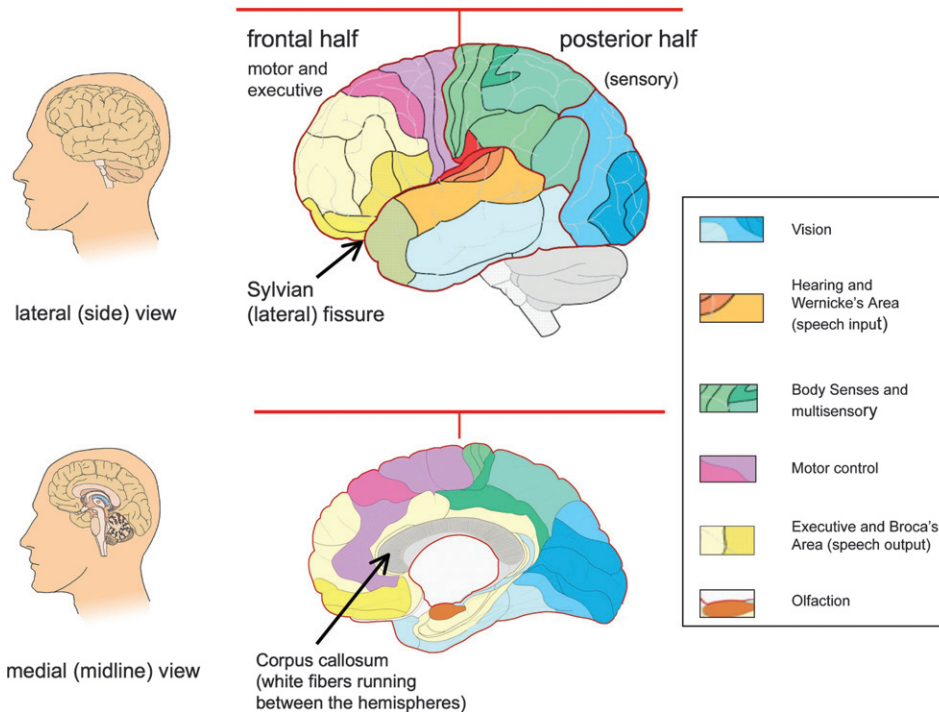


FIGURE 2.1 Functional regions of the brain. Notice the different colors and how they are labeled in the color box. Input functions like vision, hearing, and speech perception are all located in the rear half of the cortex. Output functions like motor (muscle) control, executive decision making, and speech output are located in the front half. Olfaction (smell) shows just a tiny brown area, because it is the most ancient sensory modality. It is the olfactory brain that is the seed from which the giant human brain evolved.

understanding of the brain. These two figures will help you to organize a great deal of information. We will see variations of the figures throughout the book.

2.0 COGNITIVE FUNCTIONS

Agreement on the labels for cognitive functions has emerged after a great deal of debate and data collection. Our terminology is similar to common sense, which makes it easier to remember. We will follow the definitions given in this chapter so we can use words like *memory* with the greatest clarity.

2.1 Sensory input

The left side of the framework figure shown at the beginning of the chapter shows the sensory systems. The senses all start with receptor surfaces with millions of sensitive cells arranged in flat arrays, like the retina at the back of the eye (Figure 2.2). Hearing also begins

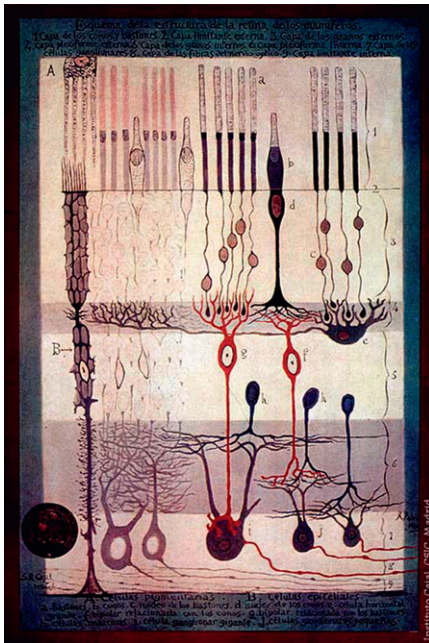


FIGURE 2.2 The retina at the back of the eye is an array of light receptors, like all the sensory systems, taking in light that is focused by the lens at the front of the eye. This beautiful drawing is by Ramon y Cajal, who discovered the nerve cell. Source: http://en.wikipedia.org/wiki/Ramon_y_cajal.

with a flat array of cells in the inner ear on the basilar membrane. The skin has a great arrays of cells, with many receptors specialized for pressure, shear (sideways force), pain, and even itching and tickling. The same is true of taste (with receptors on the tongue) and smell (receptors in the nasal cavity).

The input channels to the brain begin with flat arrays of receptors that convert physical energy into neural signals. Individual cells then send out their axons to combine into giant sensory pathways, which travel either through the spinal cord (for touch and pain) or directly through cranial nerves (for vision, hearing, taste, and smell).

Even though our eyes, ears, nose, and mouth point forward—the direction in which we move—all sensory pathways terminate in the back of the cortex, where sensory stimuli are analyzed at the highest level (Figure 2.3). We can even pinpoint the exact border between the rear half of the cortex and its front half, since there is a great vertical fold between green and purple areas in the figure, which separates input from output areas. The cortex is laid out in a way that makes sense.

Each sensory pathway reaches the cortex in its own *primary projection area*. It is easiest to remember the primary projection areas as V1 (for the primary visual projection area), A1 (for primary auditory), and S1 (for primary somatosensory cortex, the body map). V1 is an accurate copy of the retinal input (Figure 2.4). In its turn, V1 projects to higher visual maps (see Chapter 6). As the visual signal traffic flows forward, it becomes integrated with hearing, touch, body space, and motor control.

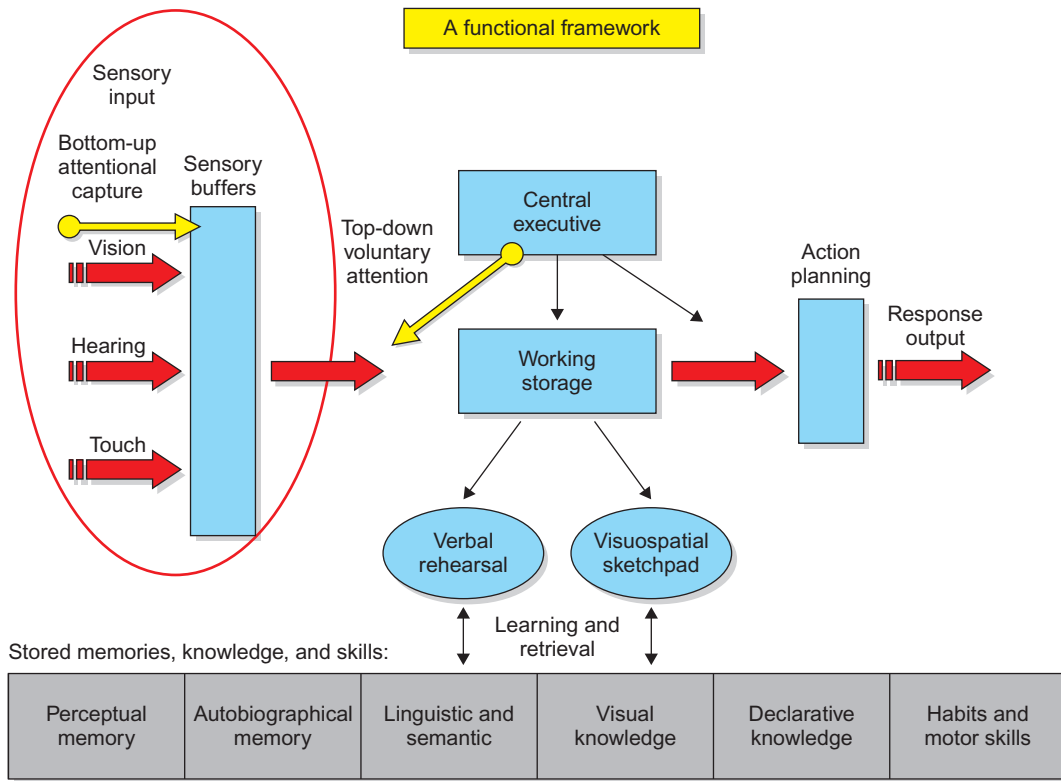


FIGURE 2.3 Sensory inputs to the functional framework. Remember that in the brain diagram of [Figure 2.1](#), the sensory cortex is the rear half of the cortex.

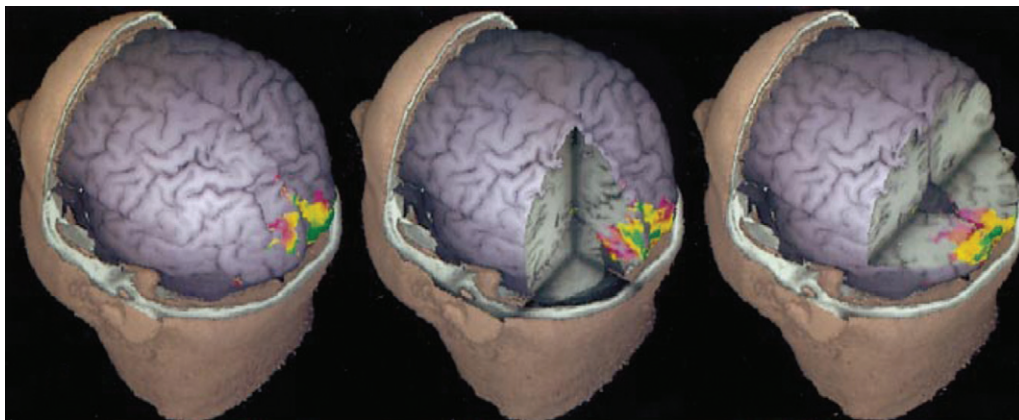


FIGURE 2.4 Occipital activation for visual stimulation. This brain scan shows activation in the occipital cortex, which is mapped point to point to the retinal light input. Source: *Singh et al., 2000*.

2.2 Sensory memories

Each of the senses has a brief holding capacity called a *sensory buffer* or *sensory memory*, shown in the functional diagram. If we close our eyes after looking at a picture, we can often “see” the picture for a second before it fades. The same kind of sensory memory applies to hearing and touch.

After sensory memory fades, it is hard to bring back a vivid experience of the original event. Sensory memories are therefore believed to reflect temporary activity in the sensory regions of the cortex, in the rear half of the brain. In our brain diagram we do not show this dynamic activity as yet, because our brain map only has the *stable* geography of the cortex, not its *active traffic flows*. This is much like the maps published by commercial airlines that show cities and regions but not the air traffic that constantly flows from point to point. Airline maps also do not show the dynamic changes in the weather at different altitudes. But the real world has dynamic as well as static properties. We will explore this point in later chapters.

Vision and audition have been studied for centuries. The body senses, like touch, pain, inner feelings (interoception), and self-perception (proprioception), are still at the frontier of brain and cognitive science. The *chemical senses* of smell and touch were the earliest to evolve, but they are not as well understood as vision and hearing. The senses are still a moving scientific frontier. New sensory abilities are still being found, including light receptors for triggering our sleep-waking cycle, a large “enteric nervous system” involved in the digestive system, and even olfactory sensing of chemical pheromones for sexual attraction.

2.3 Selective attention and conscious events

Sensory clarity is greatly improved by *selective attention*, shown by the two yellow arrows in [Figure 2.5](#). Attention has a “bottom-up” component, such as when our sensory experience is captured by a flash or a bang, or by the sight of a familiar face. We can also pay “top-down” *selective attention* if we are trying to listen to a friend in a noisy cafeteria or if we expect our favorite sports team to make an exciting move in a ball game on television. In social groups we are always drawing one another’s attention to something, using selective attention. Learning and teaching make constant use of the ability we have to direct attention to something—like our brain figures.

As we will see in later chapters, selective attention enhances brain processing of whatever is selected. We can separate “attention” into a “control” component and a “target” component, much like a spotlight that may be *controlled* by a stage manager but that is *aimed at* an actor on stage. In the brain, the control of visual attention shows marked overlap with eye movement control. This is interesting because eye movements have the same job of selecting some part of the visual field for more focal processing.

The idea that attention leads to conscious events is widely used in current science (see [Chapter 8](#)). In laboratory experiments we often talk about “attention” when there is a selective process, while “conscious experiences” are assessed by voluntary report, including naming the stimulus or pushing a button to distinguish one stimulus from another. Verbal report has been used for two centuries to map out all of the senses in exquisite detail. But the many unconscious features of the senses cannot be studied that way, because unconscious events are

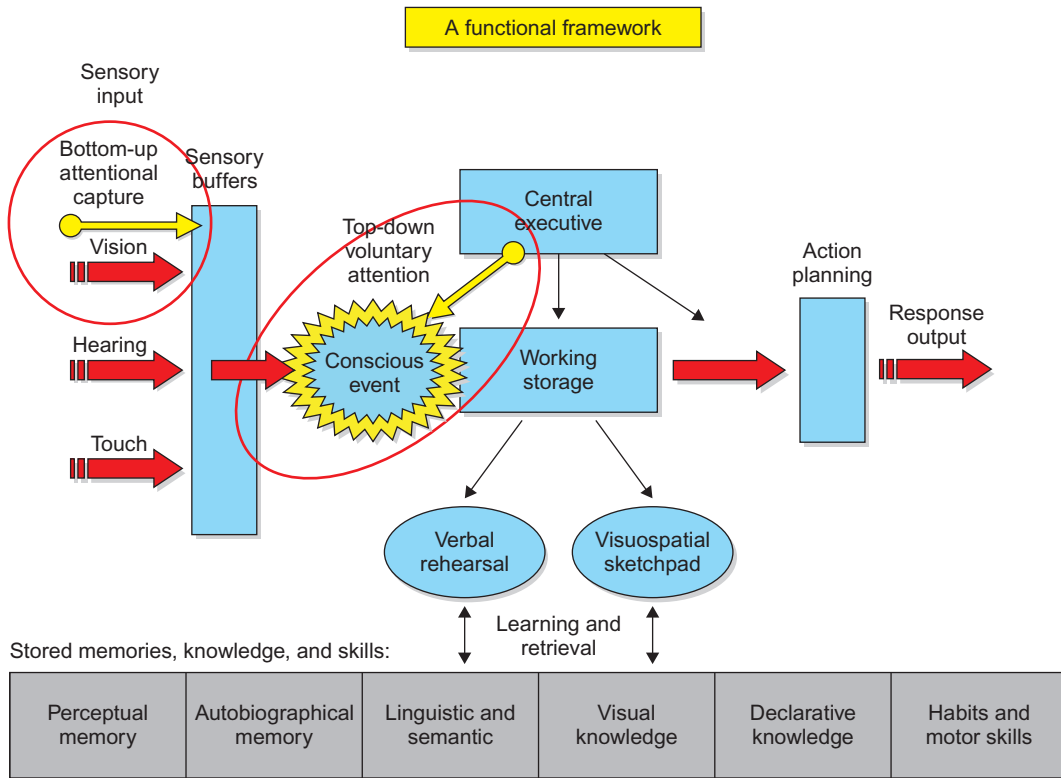


FIGURE 2.5 Attention and consciousness can be symbolized as a yellow arrow and a sunburst symbol in the functional diagram. These symbols are arbitrary, but they suggest that attention can be “aimed at” many parts of the diagram and that the result of paying attention is improved conscious access to the thing that is attended to. Both are plausible claims.

not reportable like conscious ones. We often infer unconscious brain events based on extensive behavioral and brain evidence.

One example is the long-term memories you see at the bottom of [Figure 2.6](#). Once memories are stored, they remain unconscious. We have a great deal of evidence about these unconscious archives in the brain.

2.4 Working memory

Working memory is a useful label for a number of brain functions that have a very important feature in common. Cowan and colleagues (2005) called working memory “the set of mental processes holding limited information *in a temporarily accessible state*, in service of cognition.” Notice how many boxes in [Figure 2.6](#) fit that definition. Right now you can choose to use your selective attention to look at the bottom of this page. You can talk to yourself about the figures you just saw, in your inner speech. You can decide to turn the page, a voluntary action that is shown on the right side of the framework diagram. These all fit

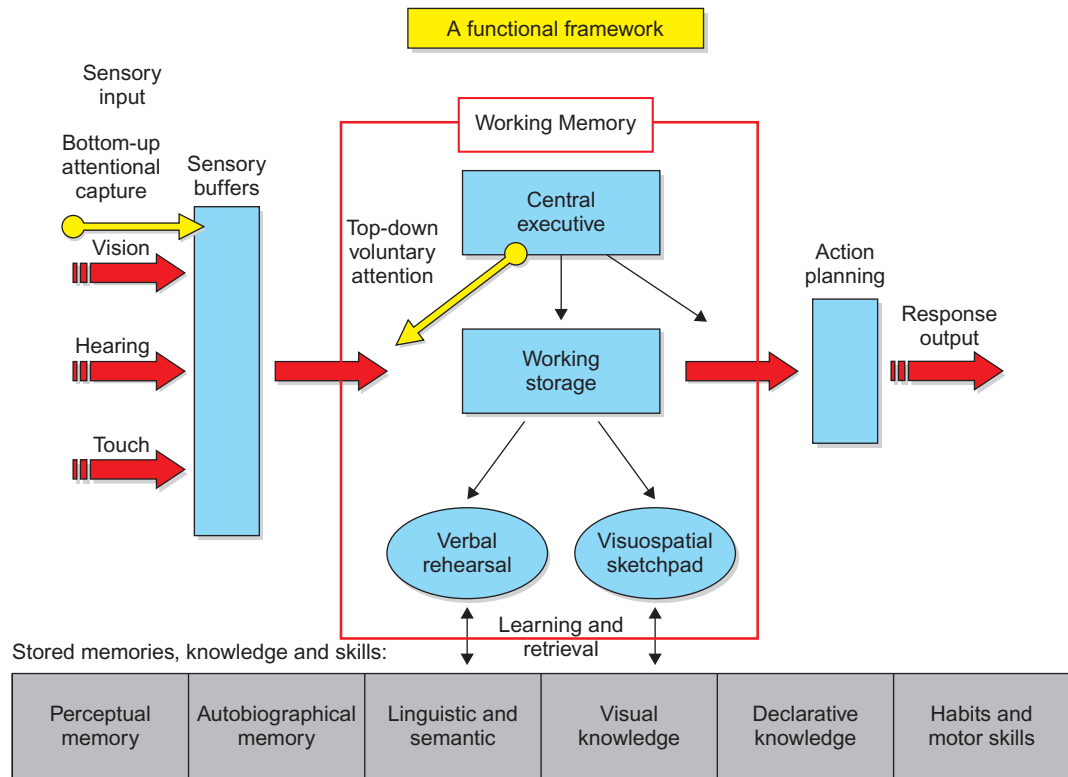


FIGURE 2.6 The working memory component of the functional diagram. The entire central column of the diagram is often called “working memory.” Cowan suggests that WM includes any kind of “limited information in a temporarily accessible state, in service of cognition.” In the brain, working memory involves activation of different cortical regions, from inner speech to visual imagery. Notice that the Central Executive is sometimes considered to be an element in WM. (e.g., Baddeley, 2000).

Cowan and colleagues’ definition. Each of those experiences are fleeting, and they are limited in capacity, meaning that you can’t do more than one at a time.

If you can rotate a mental image of a kitchen chair in your mind’s eye, that action also fits Cowan and colleagues’ definition of working memory. Remembering what you had for breakfast today and planning what you’ll do this evening also belong in working memory. All kinds of conscious and voluntary tasks have the basic properties of working memory. If you dwell on Cowan and colleagues’ definition for ten seconds, you are holding those ideas in working memory. Your ability to hold new thoughts is vulnerable to distraction, including your other thoughts and feelings. It is therefore capacity limited.

Working memory has come to stand for the many things we can keep temporarily accessible for our current goals. We can imagine mentally humming a song in order to remember the lyrics. We could call that “working memory for inner music.” Athletes can mentally practice their favorite sports, and their performance will often improve. That may be considered using working memory for running, jumping, or controlling a ball.

Scientists are now exploring types of working memory for eye movements and emotions, perhaps even for dreams. Working memory is a very general concept, and it has many uses.

2.4.1 Using working memory to access long-term memories

You can use all of the types of long-term memory at the bottom of the functional diagram by using working memory. For example, you could jump on a bicycle, and have all the old habits of balancing and steering come back in a few seconds. Or you can recall a childhood friend from autobiographical memory.

2.4.2 Talking to ourselves: inner speech

The functional diagram shows two of the “inner senses”: verbal rehearsal and the visuospatial sketchpad. These can be thought of as internal versions of outer senses. Subjectively, when we talk to ourselves, as we do most of the day, it often “sounds like” ordinary speech. Visual imagery can be vivid, like dream imagery. But a lot of our “inner senses” are not vivid. In those cases we rely on experimental methods to test whether we are indeed dealing with internal (endogenous) sources of speech and visual information.

Most human beings go around the world talking to themselves. People are often willing to tell us about their private monologue. Simply by asking them to write down clear internal speech as soon as possible, a body of useful evidence has been gathered.

The psycholinguist Gary Dell showed that inner tongue twisters evoke errors that are similar to overt tongue twisters (Dell & Sullivan, 2004). In your own inner speech, try saying, “Peter Piper picked a peck of pickled peppers” as quickly as you can. Do you notice any pronunciation errors? But you have no inner tongue to twist—or do you? Imaginary practice can be effective—which makes a lot of sense if we use similar brain regions for mental and physical practice.

Inner speech is shown as a working memory component. But it is *not* completely contained in working memory because your vocabulary was learned a long time ago and must therefore be in one of the *long-term memories* at the bottom of the diagram. Inner speech is not just for rehearsing and memorizing information; it keeps a running commentary on our “current concerns” while the vocal tract is inhibited, so we do not express our inner thoughts out loud (Singer, 1993). Because it involves the sophisticated human language capacity, inner speech is closely tied to the *linguistic and semantic* component of the long-term stores, as shown at the bottom of the diagram.

Visual imagery is easy to verify—for example, by asking people to visualize their front door and then asking them on which side their mental doorknob is located (e.g., Kozhevnikov et al., 2005). However, the “visuospatial sketchpad” also involves more abstract and *cross-modal* (cross-sensory) spatial information. For example, we can close our eyes and identify objects by touch, even though we may never have touched them before. There must therefore be cross-modal transfer between vision and touch. Such cross-modal flow of information is associated with the parietal cortex (shown in green in [Figure 2.1](#)).

The auditory sense also has a spatial component. We can locate sounds accurately with our eyes closed, especially if they have fast, high-pitched transients, like the chirps of a sparrow. Thus, all the sensory systems start off as domain-specific visual, auditory, or touch perception, but they are quickly combined in a multimodal space that represents our local environment.

We use imagery and mental rehearsal to remember new words, new faces, and spatial information, like whether to turn right at a specific street corner. There may also be “inner senses” for smell and taste, body sensations, pain and pleasure. It has been shown, for example, that *expected* pain activates brain areas that overlap with real pain areas.

2.4.3 Visual imagery

Can you remember the first time you saw the cover of this book? If you can, do any visual images come to mind? Can you bring to mind the place and the way the book looked to you? Did you see it lying flat, or was it propped up? Was it right side up or upside down? People vary in the vividness of their spontaneous mental imagery, but most people can do these tasks. Where does this happen in the brain? Figure 2.7 suggests similar brain regions are active when seeing versus imagining.

In the fourth century BCE, Aristotle suggested that visual images were “faint copies” of visual sensations; in other words, he believed that imagery was a kind of vague internal perception. In the last few decades, a mounting body of evidence seems to show he was right. The American psychologist C.W. Perky demonstrated this elegantly early in the twentieth century when she showed that people can confuse faint visual pictures with their own mental images (Perky, 1910).

There is now good evidence that *endogenous* (internally generated) events imitate the outer senses to a degree (Figure 2.8). Thus visual imagery uses many of the same cortical regions as sensory vision, as you can tell by remembering a dream; dreams are often vividly visual. If you talk to yourself (like almost all human beings do), you can hear the quality of your voice the way you would if you heard yourself speaking out loud. Dancers and musicians can often generate *endogenous* sensory experiences in order to practice music or dancing.

Stephen Kosslyn (1994) demonstrated that “the mind’s eye” is a surprisingly accurate figure of speech. The human visual field has a typical size and shape, which is easy to demonstrate. Simply look at an object in the room in which you are reading this, allowing your eyes to fixate on a point without moving your head. Now bring your hands in from the sides of your visual field until you can barely see them; the horizontal limits of the active visual field will be on the order of 120 degrees of visual arc. Do the same for the vertical limits, and it will

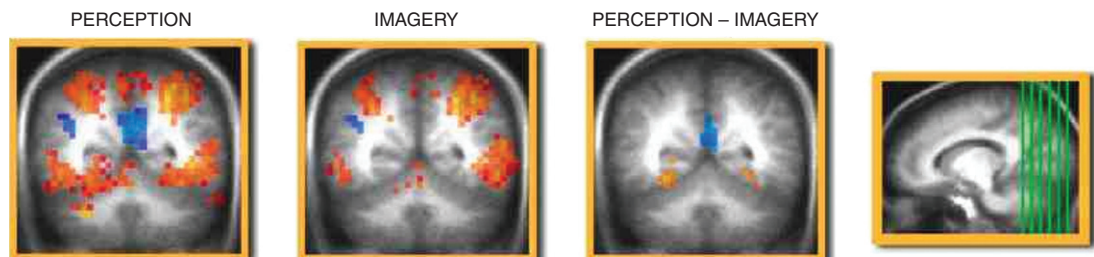


FIGURE 2.7 Visual imagery may activate parts of visual cortex. In these brain scans from Ganis and colleagues (2004), the activities for perception and imagery are so similar that they can be subtracted from each other, yielding very little difference. As the rightmost figure shows, these virtual slices were selected from the occipital and parietal region. Note that “Perception – Imagery” means “perception minus imagery” effects. The three images on the left are coronal cross-sections cut vertically through the brain, with the cerebellum visible at the bottom. On the far right, we see a medial left-facing brain. Source: *Ganis et al., 2004*.

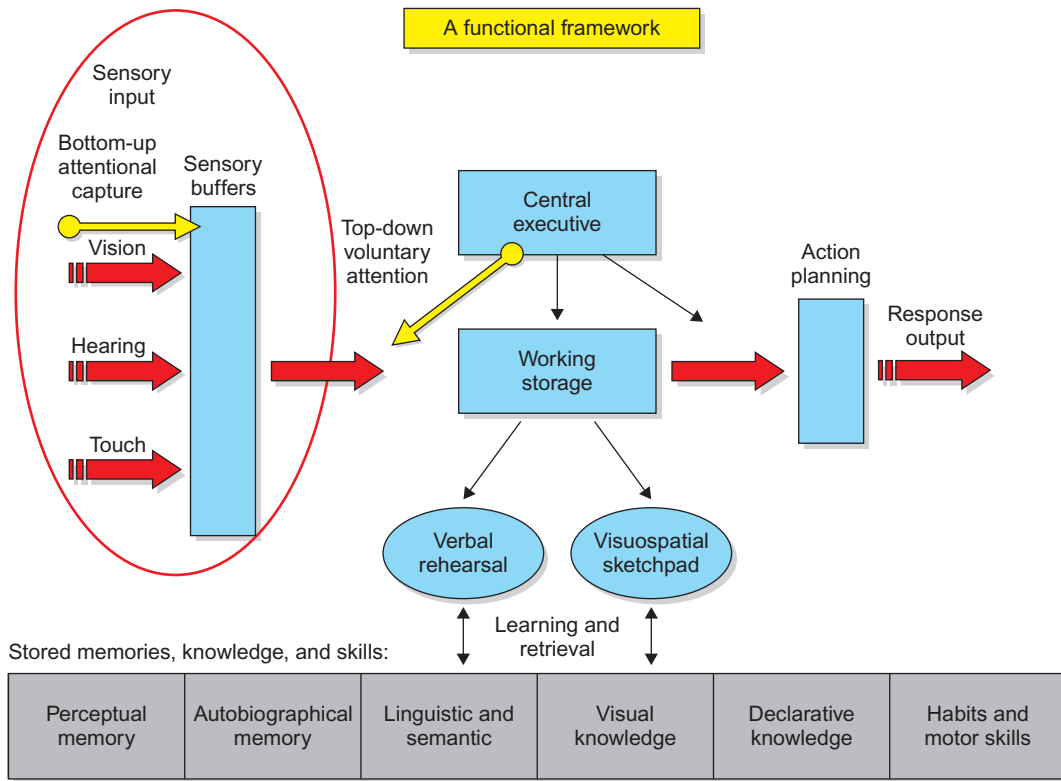


FIGURE 2.8 Framework diagram with sensory emphasis. The sensory systems receive input from arrays of receptors that transform physical energy patterns into neuronal firing. Sensory receptor arrays are then echoed at higher levels of the nervous system. In the case of vision and the body senses, there is a point-to-point correspondence between the sensory array and the early maps of the cortex.

turn out to be less than half of that. The *working* visual field seems to be a flat oval, perhaps 45 visual degrees in height by 120 degrees wide.

If you now close one eye and fix the other eye on a small target, like a single letter in this sentence, the field will shrink dramatically to only a few degrees of visual arc, corresponding to *foveal* vision. The fovea is a small, central patch of retina that has very high density of visual receptors and therefore the highest visual resolution. It is the keyhole-size “sight” that we aim at the world to get high-resolution snapshots. The fovea subtends about four degrees of visual arc.

You can measure your inner field of your “mind’s eye” in much the way you did with your visual field: by using your imaginary hands. Close your eyes, move your virtual hands to the sides of your “mind’s eye,” and write down the horizontal extent of your field. Now do the same in the vertical dimension. People generally come up with a little less than 120 degrees of horizontal arc and about 45 degrees vertical.

A variety of such experiments show a remarkable resemblance between the physical visual field and its mental double. Stephen Kosslyn, Martha Farah, and others have shown that

visual imagery elicits activity in parts of the visual cortex. Ganis and colleagues (2004) said, “Visual imagery and visual perception draw on most of the same neural machinery.”

However, there are many ways of seeing the world and many ways to use one’s imagery abilities. Depending on experimental conditions, different patterns of activity may be found in the visual cortex. By using conditions designed to match visual perception and visual imagery as closely as possible, Ganis and colleagues showed that in the brain, visual imagery can be very similar to visual perception.

Kosslyn (1994) points out that imagery “is not a unitary ability, but consists instead of a host of specialized abilities.” For example, the famous mental rotation task devised by Shepard and Cooper (1982) seems to use visual, spatial, motor, *and* executive regions (Figure 2.9).

Notice how well psychological and brain findings converge in these examples. Vision involves occipital, temporal, and parietal cortex, and so does “mental vision” or visual imagery, under carefully controlled conditions.

2.5 The brain in working memory

Notice that working memory is not located in just one place in our brain (see Figure 2.1). When you talk to yourself using inner speech, or mentally calculate 4×21 , or decide what to have for lunch, those are all working memory activities, but they engage different parts of the cortex. Working memory can therefore mobilize many capacities. The same is true for selective attention, the yellow arrows in our functional diagram, which can point to different function boxes.

Behaviorally one can assess working memory by accuracy of recall or recognition, or by the speed of responding (*reaction time*). A stimulus may be presented for a fraction of a second and then retested ten seconds later.

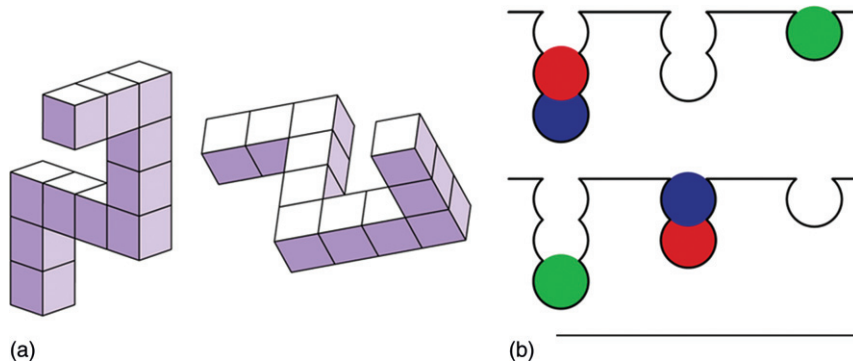


FIGURE 2.9 Different imagery tasks. (a) The classic mental rotation stimuli from Shepard and Cooper (1982). The subject is asked to report whether the two arbitrary shapes are the same or different. To answer the question, subjects mentally rotate one shape to see if it matches the other. (b) A classic “tower” task, which can be thought of as rolling colored balls from one pocket to another. How can you transform the upper picture into the lower? Here again, subjects appear to use visual imagery, but the task is quite different from mental rotation. The brain activates different regions to do the two imagery tasks. Source: *Hesslow, 2002.*

2.5.1 The surprising role of mental effort

Good science always leads to surprising findings. One of the recent surprises is the powerful role of *mental effort*. Working memory tasks can be easy or hard. An easy one is to ask a subject to remember a word they just read (like *read*). We can make that task harder by asking for the word before the last one (*last*), and so on. This “n-back” task becomes very difficult when we have to recall three or four items before the last one we saw.

Subjectively we can feel ourselves trying harder, almost as if we are rolling a giant rock uphill. Surprisingly, mental effort also has a limited capacity, so hard mental work adds up during the day, like other fatiguing tasks. As we will see later in this book, cortical activity spreads as a function of the degree of mental effort we feel.

2.5.2 Holding buffers

We have used the term *working memory* as if it were a single thing, but that is a hotly debated question. As we will see, there is evidence for both “domain-specific” and “nonspecific” temporary holding memories (see [Chapter 8](#)). Some researchers talk about working memories for concepts, for space, and for semantics, as well as vision and speech. Current evidence favors a combination of the two hypotheses: both domain-specific and nonspecific working memory capacities are present.

2.6 Long-term memories

Long-term memory stores are shown in the bottom row of boxes in [Figure 2.10](#). These are the memory systems for autobiographical episodes, for various kinds of knowledge, and for highly practiced expertise. Once these memories are stored, they are not conscious. However, they can be retrieved from memory and again enter into the memory ([Figure 2.11](#)).

Long-term memory traces are located in many places, as we will see. These may include the entire cortex and subcortical structures like the basal ganglia and cerebellum. But almost everything we can see in [Figure 2.1](#) is the more recent cortex, called the *neocortex* (the more recent mammalian cortex, as opposed to the ancient cortex of reptiles and earlier vertebrates). Neocortex has expanded greatly over mammalian evolution, accelerating during primate and hominin evolution over the last 4 million years.

2.7 The central executive and voluntary control

Working memory is often said to include a *central executive*, the subject of much current research. The central executive has been extensively studied in learning tasks. However, it now includes supervisory control over all voluntary actions (e.g., Luria, 1976; Goldberg, 2001a, 2001b). The central executive is strongly associated with the frontal lobes in our brain diagram (see [Figure 2.1](#)). [Figure 2.12](#) shows where the central executive fits into our functional framework. It is close to what we mean in everyday language by the “self” or what we refer to as “I” and “me.” Science tends to avoid everyday language like that—at least until scientists feel entirely sure that everyday terms are solidly based in evidence and theory. For that reason, terms like *central executive* are currently preferred. One reason for the careful use of

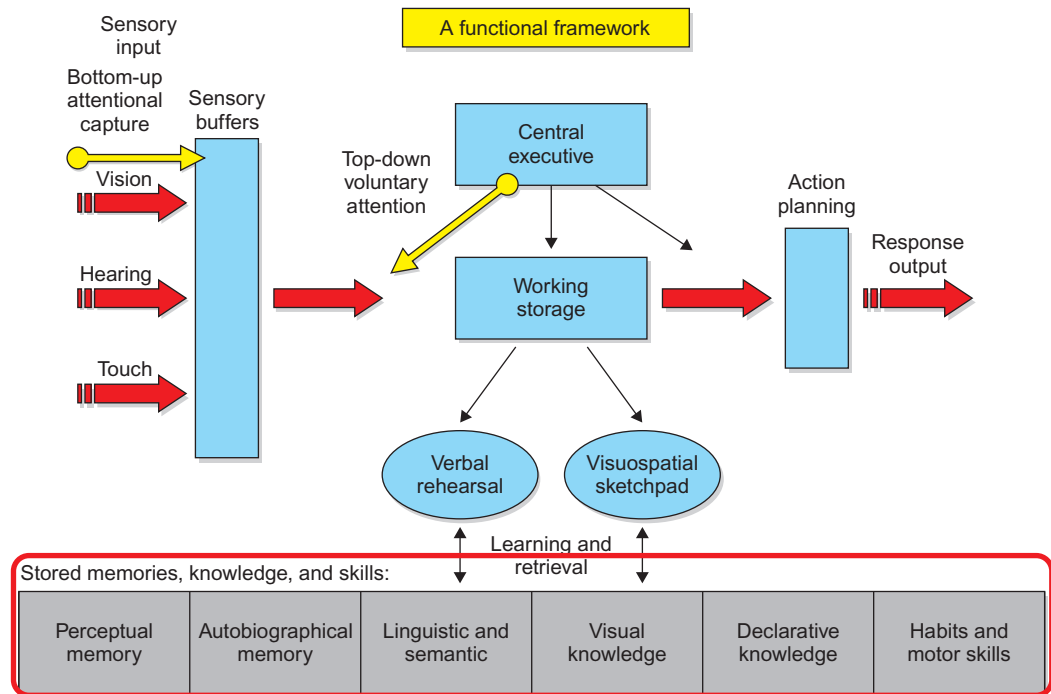


FIGURE 2.10 Emphasizing long-term memories. Notice how many varieties of long-term memories exist. It is currently believed that all brain regions may have their own capacity to store long-term traces by growing synaptic links between neurons. Thus the cerebellum is involved in learned eyeblink conditioning. Perceptual memory involves permanent changes in the sensory cortex. Habits and motor memory involve the basal ganglia. These permanent memory systems do not load the limited-capacity system. They are believed to result from overnight consolidation of material learned in the preceding conscious waking period.

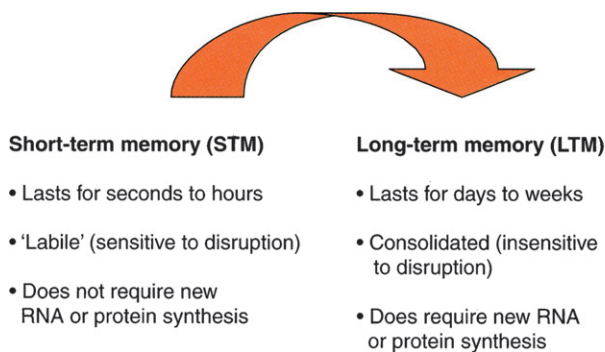


FIGURE 2.11 How immediate memory is believed to change into long-term memory traces.

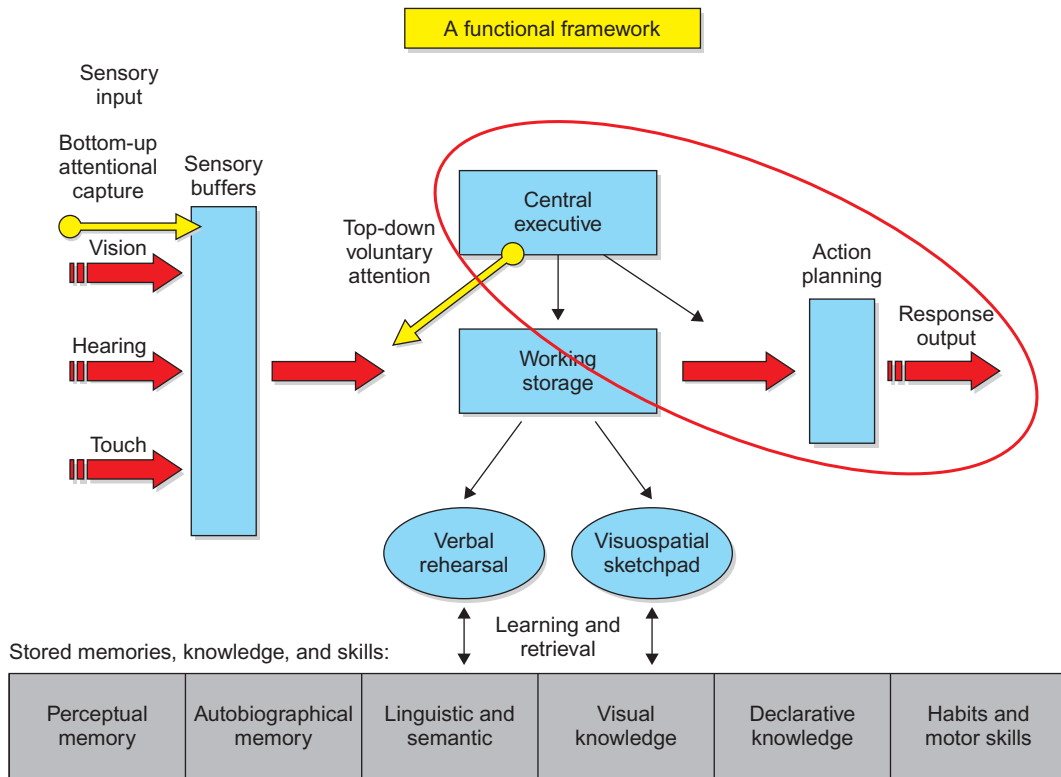


FIGURE 2.12 Executive control, action planning, and response output in the functional diagram.

language is that the central executive has so many functions. The evidence has emerged over a period of decades. Because science always moves carefully, step by step, we will use the standard terminology in this book.

The central executive is a useful metaphor for a chief executive officer of an organization. Mateer and colleagues (2005) said the following:

Imagine the role of the executive of a large company, who has overriding control over the company's actions. This person sets goals, plans and organizes company activity to meet those goals, and decides when to start to do something, when to stop doing it, when to do something else, and when to do nothing at all.

The executive is *future directed* and *goal oriented* and, to be effective, must be *flexible* and *adaptive*. At a basic level, this is what the prefrontal cortex does for humans. (*Italics added*)

The word *prefrontal* means the forward part of the frontal lobes. Prefrontal executive regions are located in front of the purple motor regions of the brain (see [Figure 2.1](#)). They are marked in light beige and yellow on both the outside and inside of the hemispheres. Notice that Broca's area, first discovered in the nineteenth century, is technically a part of the prefrontal cortex. However, the light purple motor regions also have some executive functions. These boundaries are not absolute, but they are useful as a first approximation. Later chapters discuss executive functions in more detail (see [Chapter 12](#)).

2.7.1 The executive brain

On the right-hand side of our functional diagram are the output functions involving the control of voluntary actions, including speech. These include the *central executive*, *action planning*, and *motor output*. For the purposes of our diagram we only show voluntary motor functions, the ones that control our skeletal muscles—the muscles of the limbs, torso, head, and face.

As mentioned before, the prefrontal lobes play an important executive role in the brain. They are needed for voluntary control over actions. Prefrontal regions also support emotional processes and seem to be necessary to control one's own unwanted impulses. The neurologist Oliver Sacks writes (in Goldberg, 2001b):

The frontal lobes are the latest achievements of the nervous system; it is only in human beings (and great apes, to some extent) that they reach so great a development. . . . They lack the simple and easily identifiable functions of the more primitive parts of the cerebral cortex, the sensory and motor areas . . . but they are overwhelmingly important. They are crucial for all higher-order purposeful behavior—identifying the objective, projecting the goal, forging plans to reach it, organizing the means by which such plans can be carried out, monitoring and judging the consequences to see that all is accomplished as intended. . . . Without the great development of the frontal lobes in the human brain (coupled with the development of the language areas) civilization could never have arisen.

Damage to the frontal lobes can therefore have devastating effects on our ability to control our own emotional impulses. This was the case with Phineas Gage, a railway foreman who, while setting an explosive charge in 1848, had a two-foot tamping iron blown through his frontal lobes when the dynamite charge backfired. If you look carefully at [Figure 2.13](#), you can see that the iron rod miraculously flew between the two hemispheres at the front, thereby

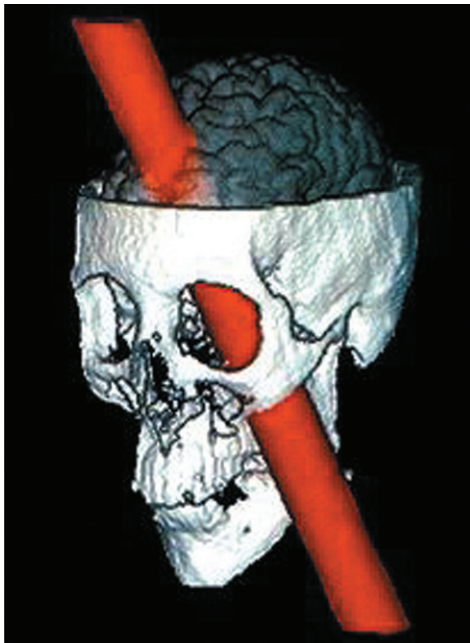


FIGURE 2.13 Phineas Gage changed personality after injury. Hanna Damasio's computer reconstruction of the brain damage suffered by Phineas Gage in 1848, based on his death mask (Damasio et al., 1994). At the time, most victims of such accidents died from an infection of the wound, if not from brain damage and blood loss. Gage was fortunate to survive and recover most of his abilities, but he could no longer pursue his old life goals or control impulsive actions. These changes were so profound as to signal a change in personality. Similar phenomena are observed in other cases of frontal lobe injury. Source: Caplan and Gould in Squire et al., 2002.

doing less damage than we might expect. Gage therefore survived the accident, but he lost frontal lobe functions. His intelligence was preserved, as well as his ability to move, talk, and see. But there were other, profounder changes in his personality. Gage became reckless and improvident, impulsive and profane. He could no longer plan for the future, and to his old friends, “he was no longer Gage.” He had lost his ability to exercise self-control. As in many patients with damage to the frontal lobes, he also did not realize he was impaired.

The Stroop Color-Naming Task is commonly used to test for frontal lobe damage. In the Stroop task, a conflict is set up between reading a word and naming its color. By using printed color names, we can present the word “blue” in a green color and ask people to name only the colors as quickly as possible (Figure 2.14). Since educated people are highly practiced readers, their automatic tendency is to *read* the word rather than name its color. The task instructions therefore ask them to do the opposite of what they have practiced doing for many years. In people with healthy brains, the Stroop task sets up a conflict involving prefrontal cortex, but it can usually be resolved. Response times are slowed compared to a control condition, and people sometimes make errors. But in frontal lobe patients, the effects of the conflict are more debilitating, leading to more errors, longer response times, and a greater sense of subjective difficulty and frustration. The Stroop Task is useful to probe for subtle frontal lobe damage that may be missed by brain scans.

2.7.2 The voluntary muscles: what we can control

Humans have at least two different muscle systems. One system is called “voluntary” because we can control those muscles at will and on request from others. These are the cranial and *skeletal* muscles, the ones that control our bodies and heads. Our hands, arms, legs and toes, and torso are under voluntary control. Our facial muscles are also voluntarily controlled

BLUE	GREEN	YELLOW
PINK	RED	ORANGE
GREY	BLACK	PURPLE
TAN	WHITE	BROWN

FIGURE 2.14 Volition vs. automaticity. The Stroop Color-Naming Task reflects executive functions. Try to name the colors on top, and you are likely to find it difficult. When the words are upside-down, and therefore harder to read, color naming is easier, faster, and more accurate (bottom half). Source: Miller & Wallis in Squire et al., 2003.

ТАИ	МНІЕ	ВЪОМИ
СВЕУ	ВГАСК	ЪУВЪГЕ
ЫИК	ВЕД	ОВАНСЕ
ВГНЕ	СВЕЕИ	ЛЕГГОМ

via nerves that run through tiny holes in the cranium. They are the “cranial muscles.” Because speech muscles are located (mostly) in the head, they are part of the same voluntary control system.

The “smooth muscles” of our digestive and circulatory systems are not under voluntary control. These are part of the autonomic nervous system, which is “autonomous” from any efforts we make to control it. We cannot directly control our heart rate, for example, or the sweat glands of our fingers. The emotions make great use of both voluntary and autonomic muscles.

Likewise, we can take a deep breath “at will,” but we normally breathe in a spontaneous and automatic way. Large eye movements can be controlled voluntarily as well as automatically. For smiling, breathing, and eye movements, automatic control is much more common than voluntary cortical control. As we will see, selective attention also has dual control, both voluntary (executive) attention and spontaneous (attentional) selection.

Such dual control is a common strategy of the brain, but it does not apply to vital functions, like control of the heart rate. For obvious reasons, heart rate control is automatic; it would be disastrous to try to stop or start it at will. The same is true for other autonomic functions.

Brain injuries can sometimes *dissociate* voluntary and automatic control centers from each other, as happens in disorders that impair only voluntary smiles, but not spontaneous ones (Figure 2.15). There are also brain lesions that work the other way: damage to the brainstem can cause automatic control to be disabled while voluntary control is spared.

The voluntary system is controlled from the frontal lobes, the executive control system. Autonomic muscles have indirect connections to the cortex, but they are mostly controlled from the brainstem and spinal cord, and from local nerve centers located in the heart and stomach. This is important, because voluntary control can be crude, and we don’t want to tell organs like the heart or stomach exactly what to do when autonomic control works so well.

There are also *dual control* systems that combine voluntary control with nonvoluntary nerve centers in the brain and spinal cord. If you stumble and fall forward, your hands



FIGURE 2.15 A brain injury that separates voluntary and spontaneous smiles. On the left, this patient cannot make a symmetrical smile, while on the right her smile looks quite normal. On the left, she is trying to smile voluntarily, while in the right photo she is smiling spontaneously. The damage to her frontal lobe motor regions does not affect her (subcortical) facial expressions. Other patients show the opposite damage, impairing spontaneous smiles but not voluntary ones. The ability to show that two brain functions can be damaged independently of each other is called a double dissociation. Source: Paxinos & Mai, 2004.

and arms immediately shoot forward to protect yourself in the fall. That is not a voluntary act but a nonvoluntary reflex. However, you could do the same action voluntarily. Such actions have dual control.

Dual control is especially important for facial emotional expressions. We smile spontaneously when we hear a funny joke, and we try to smile as much as possible when a guest drops a glass of red wine on our favorite white carpet. The voluntary smiles are “social smiles” that we display to show our friendly intentions, even if we don’t feel like it. Both kinds of smiles are extremely important to us as social creatures.

Other facial expressions like frowns and “surprise!” faces are also under dual “voluntary plus spontaneous” control. Spontaneous facial expressions are often under the control of brainstem centers, which are quite separate from the executive functions of the frontal lobes.

We also have some voluntary control over spinal reflexes, like the famous knee-jerk reflex, but in that case the frontal lobes mostly *inhibit* the spinal circuit. If you hold your leg rigidly while someone taps under your kneecap (the patellar tendon), you can stop your lower leg from kicking outward. But if you stop paying attention and you accidentally hit your patellar tendon against a table, your lower leg will kick out in spite of belated efforts to control it.

Many brain activities are not under voluntary control, including cravings (for food, water, or addictive substances), homeostatic mechanisms (like blood oxygen control), and our own emotions when they are intense or surprising. Sensory processes are not under voluntary control as a general rule, but in many cultures people learn not to look at others to avoid confrontation or unwanted sexual signaling. Eye movements are therefore also under *mixed* voluntary and involuntary control.

Numerous disorders interfere with normal control. Patients with Parkinson’s disease cannot control their voluntary muscles as precisely as they want to. Certain kinds of aphasics (people with language impairments) cannot say what they desperately want to say. People with Tourette’s disorder have the opposite problem, saying things they *don’t* want to say.

All the “functional disorders,” like depression, excessive anxiety, obsessive-compulsive disorder, or impulse control problems, are marked by either undercontrol or overcontrol in executive functions. The actual locus of the problem may be in the frontal lobes or in lower-level control levels like the cerebellum, basal ganglia, brainstem, or spinal cord.

There is a debate about whether voluntary actions are equivalent to consciously decided ones (Schneider, 1995; Shiffrin et al., 1995). This is a difficult issue to settle. However, there is little disagreement that voluntary control and conscious cognition tend to go together. In sum, executive functions are extraordinarily important.

2.7.3 Executive effort and automaticity

Voluntary actions become automatic with practice (Shiffrin & Schneider, 1977). As they do so, we also tend to lose some executive control over them (e.g., Langer & Imber, 1979). Our loss of control over highly practiced and predictable habits seems to go along with a loss of conscious access to their details (Schneider, 1995). In brain scans, we see a dramatic reduction of cortical activity when a voluntary action is practiced to the point of automaticity (Figure 2.16).

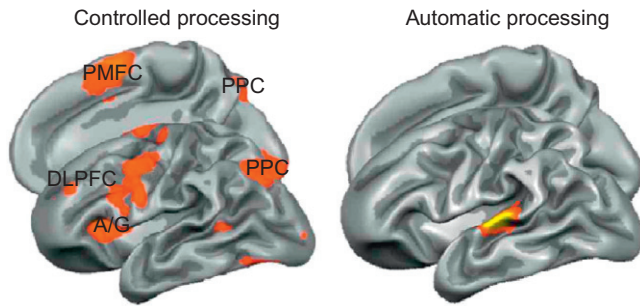


FIGURE 2.16 A dramatic difference in cortical activity between a novel and a practiced (automatic and unconscious) task. On the left, the brain during visual face recognition and auditory search for a sound. Notice how many areas are activated (red). On the right, the identical task after enough practice to make it automatic, and therefore nearly unconscious. Only the auditory region still shows activity. Source: Schneider, 2010.

Routinized voluntary actions may be taken over in part by subcortical regions, notably the basal ganglia and cerebellum.

However, we should not make an all-or-none distinction between voluntary and automatic actions. Automatic actions can come under voluntary control again when predictable aspects of the action become unpredictable, such as when we break a leg and try to walk in our usual way (Sacks, 1984). Most everyday activities are a mixture of voluntary and automatic control. The most highly practiced components of our habitual actions tend to be automatic, while the most novel and unpredictable ones tend to remain under voluntary control. Thus we may be able to make voluntary decisions about which way to walk at a new street intersection, but once we decide to turn right, we are rarely conscious of each step we take. The same general point applies to speaking, reading, eye movement control, and much more. Automatic and voluntary control work hand in hand.

2.7.4 The input and output hierarchy

There are some striking parallels between perception and action. Fuster (2003) points out that both input and output can be viewed as processing hierarchies. The visual hierarchy begins with retinal “pixels” in cortical area V1, the primary visual cortex, and proceeds to areas specialized for color, motion, and object recognition (see [Chapter 6, Figure 6.10](#)). On the output side, the motor hierarchy begins with general goals, influenced by emotional and motivational input from limbic regions. The most general goals are represented in more prefrontal areas and proceed down the motor hierarchy to supplementary and premotor regions that may trigger intentions and the urge to act (e.g., Penfield & Roberts, 1959). The primary cortical motor region (M1) directly triggers the movement of skeletal muscles.

[Figure 2.17](#) shows brain regions that become active in pushing a button with the right hand. The lower right panel shows a time scale marked in seconds, and anticipatory brain activity begins several seconds before the finger press. Notice that motor cortex is active on the *left* side, opposite to the hand that is commanded to move (this is called the *contralateral* side). However, motor cortex activates cerebellar activity on the *same* side as the moving hand (*ipsilateral*) until finally the finger press occurs at the zero point in the time scale.

Humans also have voluntary control over some mental functions. A good example is verbal rehearsal and mental rotation of a visual image. If you can visualize a kitchen chair, you

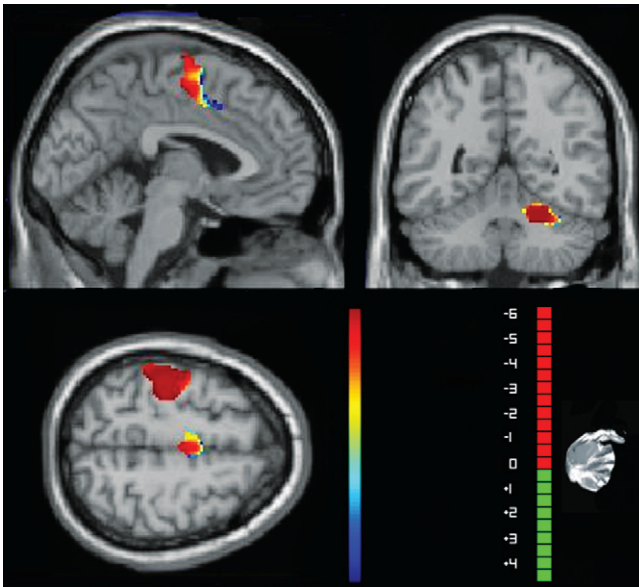


FIGURE 2.17 What the brain does to push a button. Hulsmann and colleagues (2003) showed how the voluntary goal of pressing a button rises over seconds before action. This snapshot shows the target time (time zero) when the finger press occurs (lower right). The two scans on the left show activation in motor regions of the left hemisphere, which controls the right hand. However, the upper right image shows activation on the right side of the cerebellum, which is required for fine motor movements like finger presses. This crossover activity is consistent with the known anatomy of motor control. Source: *Hulsmann et al., 2003*.

may be able to turn it upside down mentally. This kind of imagery task activates motor, spatial (parietal), and visual cortex. Because it is voluntary, it is believed to be controlled by frontal regions.

2.7.5 Speaking

It was the French physician Pierre-Paul Broca (Figure 2.18) who first discovered a region of the left hemisphere tied to language production, a higher mental function. The “speaking” region of the left hemisphere is therefore called Broca’s area.

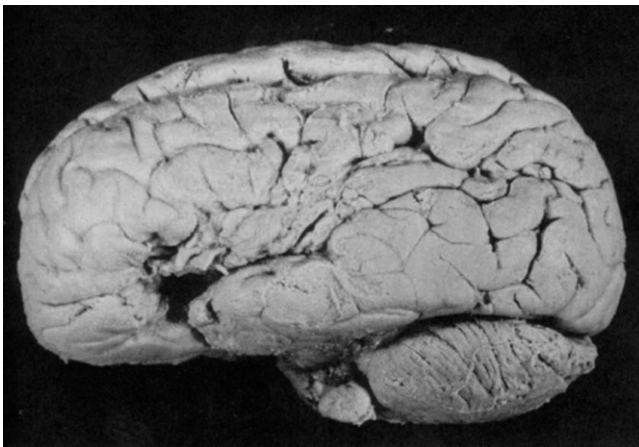


FIGURE 2.18 The brain of Broca’s first aphasia patient has been preserved. If you look at the frontal region of the left hemisphere, you can see a large hole in “Broca’s area.” Broca’s region is now believed to control speech production as well as other integrative executive functions. Source: *Ramachandran, 2002*.

Controversy has raged over brain localization—whether specific regions of the brain serve specific functions. Broca was the first to prove a specialized region of the higher brain in 1861. Broca’s patient had lost all ability to speak except the single word “tan.” After the patient died, Broca was able to perform an autopsy, finding “damage to the posterior part of the third frontal convolution in the left hemisphere.” You can see the location of the damage in the frontal region of the left hemisphere (see [Figure 2.18](#)).

Six months later, Broca presented a similar case, again with damage to this part of the left frontal lobe. Despite criticisms that other areas of the brain were involved and that some patients with similar disorders did not have frontal lobe lesions, Broca’s observations came to be accepted because of the weight of the evidence. Today, Broca’s area in the left frontal lobe is widely recognized as a critical component of language (Aminoff & Daroff, 2003).

Much of what we know about the human brain was first discovered from specific types of brain damage. That effort continues today. Another important finding for language was made by Carl Wernicke, who discovered a patient who could say more than just one word, but without being able to understand speech. Today, Wernicke’s area in the temporal lobe is widely recognized as an important brain area for receptive language. Patients with brain damage in this region and deficits in speech comprehension are still called “Wernicke’s aphasics.”

Here is a speech sample from a modern patient (FL) with receptive aphasia, due to damage in or near Wernicke’s area (Dronkers & Ogar, 2003):

Examiner: “Tell me what you think your problem is.”

FL: “Ah, where do I start the tesseinemen from? They tell me that my brain, physically, my brain is perfect, the attitudes and everything is fine, but the silence now, that I have to reeh-learn through edgit again, physically nothing wrong with it. It’s perfect the doctors tell me. They have attitude. Physically I have loozing absolute nothing on my head, but now I have to go through these new attitudes to looalize how, some, how can I say to? Some what that I can reeh-learn again so I can estep my knowledges, so th’you kyou again, what how can I say that y. . . .”

Notice that this patient is much more fluent than Broca’s classic patient of 1861, who could only pronounce one syllable. However, this patient’s ability to comprehend meaningful speech is impaired.

The internal mass of the cortex is *white matter*, consisting of billions of axons emerging from the gray cell bodies in the surface layers of the cortex. Those axons are wrapped in white myelin cells, filled with fatlike lipid molecules. They therefore look white to the naked eye. Most of the white matter therefore consists of great fiber bundles, connecting every region of cortex to every other, like some great highway system. Careful anatomical dissections showed a fiber bundle connecting Broca’s and Wernicke’s areas in the left hemisphere. These fiber bundles are known as *arcuate fasciculi*, Latin for “arched little bundles.” (Again, an everyday Latin term has become a long and complicated word to our ears.)

Based on this evidence, Wernicke was able to predict a new language deficit called *disconnection aphasia*. If the fibers between Broca’s and Wernicke’s areas were damaged, he thought, patients should have difficulty *repeating* speech sounds—transferring information from the receptive area (Wernicke’s) to the production region (Broca’s). That prediction was borne out ([Figure 2.19](#)). It is believed that there are a number of such disconnection syndromes. A number of aphasias are thought to exist.

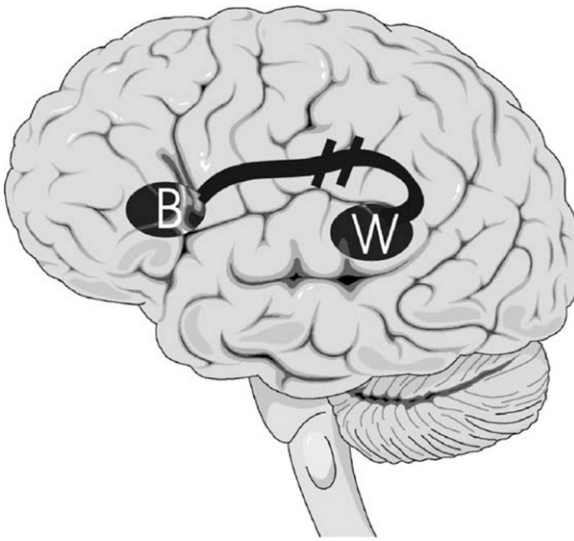


FIGURE 2.19 Conduction aphasia. Careful anatomical dissections showed a fiber bundle connecting Broca's and Wernicke's areas of the left hemisphere. Based on this evidence, Wernicke was able to predict a new language deficit called "disconnection aphasia." If the fiber bundle between Broca's and Wernicke's areas were damaged, he thought, patients should have difficulty transferring information from the receptive area to the productive region. Source: *Dronkers & Ogar, 2003*.

Notice that language areas usually exist in the left hemisphere (see [Figure 2.19](#)). Modern evidence shows that the right side of the brain can perceive language, but it does not control vocal output. The right side is believed to be sensitive to the emotional content of language, such as humor and irony. Left-side language dominance seems to apply to about 90 percent of the population.

3.0 USING THE FUNCTIONAL DIAGRAM

To see how the functional framework can be used, we will consider an important case of brain damage: the case of a man who lost his ability to turn his fleeting moment-to-moment experiences into lasting memories.

3.1 Only a fleeting moment

One day in 1985, a rising young musician in Britain realized that he could not remember his wife's name. That same evening, Clive Wearing tried to remember the names of his two children and failed ([Figure 2.20](#)). Deborah and Clive Wearing had been married shortly before the onset of his condition, but he could not remember his wedding. His condition, which was permanent, came on without warning after two days of severe headaches and fever. That was long enough for a viral infection to destroy regions that are needed for new memories to form.

Wearing was stricken with chronic, dense amnesia of unusual severity, including both *episodic* memory loss—he could not remember past experiences—as well as a partial loss of *semantic* memory—an inability to understand some domains of meaning (Wilson et al., 1995). Most crucially, he was unable to learn new information. His life, as his wife Deborah later said, was suddenly narrowed to “a single, blinkered moment,” with no future and no past.

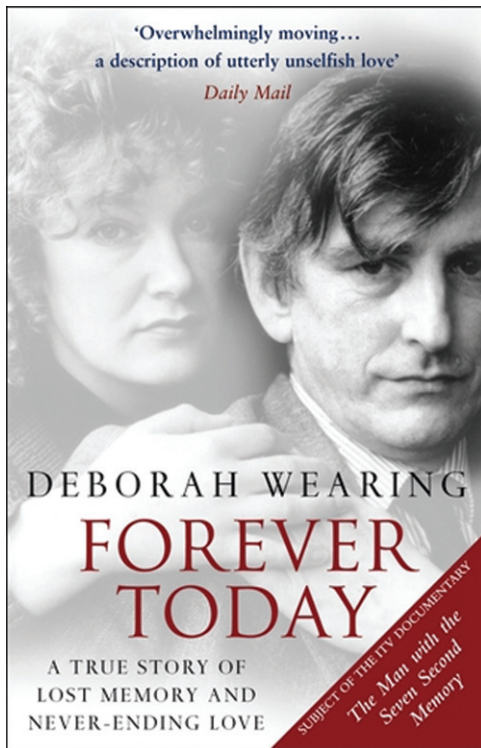


FIGURE 2.20 Clive Wearing: Loss of episodic learning and recall. After losing both hippocampi, Clive Wearing was still able to play piano and conduct musical pieces that he knew before the injury. However, he could not learn new episodic (conscious) events. Wearing could retain conscious experiences for perhaps 10 or 20 seconds. However, he was catastrophically impaired for episodic learning—that is, for transferring conscious information into long-term episodic memory. Source: Wearing, 2005.

Clive Wearing has now been the subject of 20 years of news stories and television documentaries. He seems unchanged as a person. He is fully conscious of the immediate world around him, can read and write, and can carry on a conversation in the present moment. Wearing can even conduct his small chorus if he knows the music. He is an emotionally intense person, maybe even more than before his injury, especially in his feelings for his wife Deborah.

Clive Wearing lives in an eternal present. For the first eight years, he spent every day in his hospital room writing in his diary. Every few minutes he wrote down the time of day, followed by the exclamation, “I am now conscious for the first time!!” A few minutes later he would often cross out the entry, believing that he had not really been conscious at all because he could not recall that moment.

The same routine was repeated thousands of times, filling numerous diaries. When Wearing’s wife or friends came to visit, he greeted them as if he had never seen them before. If they left for a few moments, Wearing could no longer remember their visit. Even today, whenever Wearing sees his wife Deborah, he believes he has not seen her for a long time. (Wearing, 2005).

We know more about Wearing’s life than about others with similar damage. However, by far the most scientific studies have been conducted with a patient we know as HM who was first studied by Brenda Milner and Herbert Scoville (Scoville & Milner, 1957).

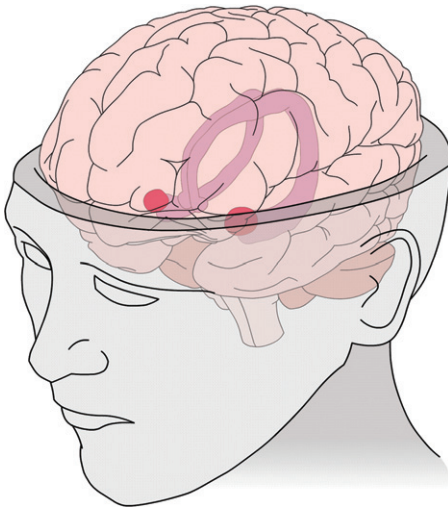


FIGURE 2.21 The hippocampus is wrapped in the temporal lobe on both sides. A see-through image of the cortex with the hippocampi nestled inside the temporal lobes. The red bulbs near the tips are the amygdalas, which play a fundamental role in emotion. Surrounding areas of the medial temporal lobe (MTL) also play important roles in memory. (See [Figure 2.24](#).)

In the 1950s, there were few drugs to prevent epileptic seizures. A treatment of last resort for severe, untreatable epilepsy was the surgical removal of part of the temporal lobe. In the case of HM, the two hippocampi and some surrounding regions were removed on both sides ([Figure 2.21](#), [Figure 2.22](#)). Careful studies over decades showed that HM was unable to store new autobiographical episodes—memories of his conscious life experiences. However, HM was able to learn new sensorimotor skills (procedural memories). Like Clive Wearing, HM’s ability to understand language and basic events was largely left intact. Thus, his *semantic memory* was not seriously impaired.

The idea of basic differences among autobiographical (episodic), procedural, and semantic memory emerged over many years of study. In addition to these memory types, our brains have large *perceptual memory capacities*, long-lasting changes in our ability to perceive the world. Learning to hear musical instruments in a new song may involve new perceptual memory capacities. As children grow, their ability to perceive speech, visual objects, faces and voices, all become part of their permanent perceptual memories. In the case of Clive Wearing, his trained capacity to perceive and enjoy music does not seem to be impaired. (Experienced musicians can perceive more aspects of a musical piece than novices; that is, their cortical regions in music perception and performance tend to be highly developed.)

There are other long-term capacities. Humans have a vast amount of knowledge about their native language, their culture, and the surrounding world. Educated speakers of English can understand some 100,000 words, and each word involves a network of associated knowledge. We have expert skills in processing grammar, discourse, and the interpersonal world. Most of this knowledge is unconscious at any given time (Bargh, 2006). As far as we know, Clive Wearing’s linguistic and semantic knowledge is unchanged, even with his severe brain damage.

Humans live in a rich visual world. We know that an egg can fall from a table and break, but a table does not usually fall from an egg and break. The oddity of the second idea reflects

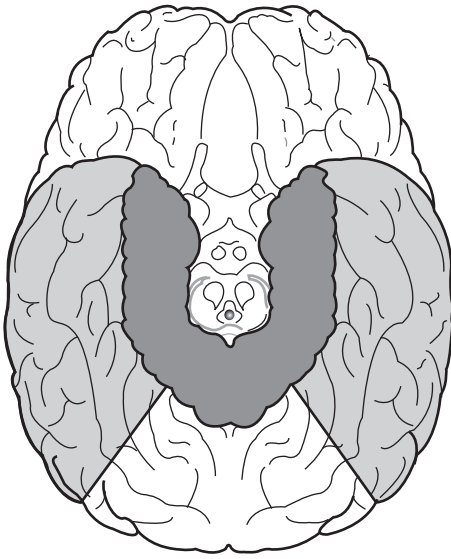


FIGURE 2.22 The surgical drawing of HM's operation. A bottom view of the brain shows regions removed by surgery in HM. It is now usual to refer to the entire medial temporal lobe (MTL), which is marked in dark gray in the drawing. The term "medial" refers to the midline of the brain, running from front to back.

our unconscious knowledge about the world. We have no reason to believe that Clive Wearing's and HM's visual knowledge is impaired.

Finally, *declarative knowledge* is defined as our ability to learn and recall facts and beliefs. It includes the things we learn in school, which can be "declared" as propositions about reality. "China is a large country," "Whales are marine mammals," and so on. Again, there is no indication that hippocampal damage impairs established declarative knowledge.

It seems that *existing* knowledge and memory are largely left intact with hippocampal patients like HM and Clive Wearing. And yet, according to Deborah Wearing, her husband's life was devastated. His greatest loss was in his capacity to learn and bring back his everyday experiences.

3.2 HM and Clive Wearing

Notice that most mental functions are *not* lost in hippocampal damage. Clive Wearing seems to have normal conscious sensory experiences, including his ability to appreciate music. His voluntary (executive) control seems normal, and so does his muscle control. As we pointed out, some types of long-term memory seem to be unimpaired, except for his inability to store and retrieve his autobiographical experiences. Wearing speaks and understands language with no impairment. In most tests of intelligence he may score well.

Clive Wearing's losses, therefore, are not in most of the boxes of the functional diagram. His deficit seems primarily in the *transfer of information* between immediate memory and long-term memory, in both directions: between encoding conscious experiences and retrieving them (Figure 2.23).

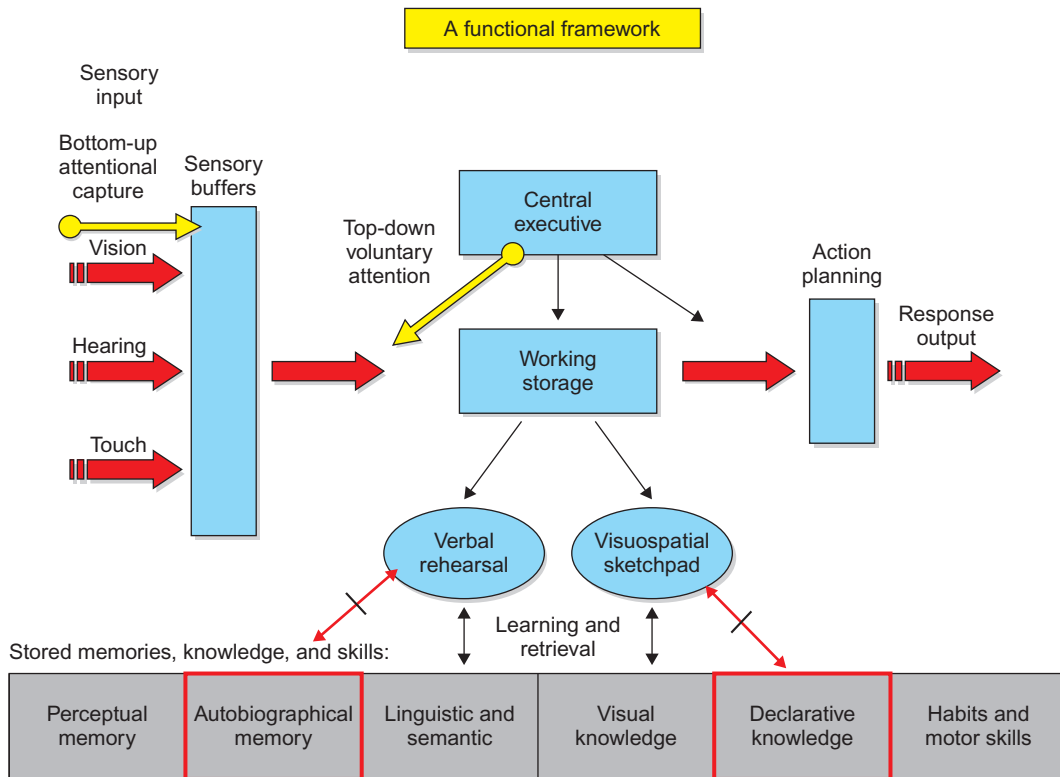


FIGURE 2.23 Notice that damage to the hippocampus does not impair most cognitive functions. As the red lines and arrows show, patients cannot acquire or recall new autobiographical (episodic) memories. To patients, these losses can be devastating.

3.3 What is not lost?

Sensory and working memory are needed even for the simplest activities. If you cannot remember the *beginning* of this sentence, you cannot understand its *ending*. Because a sentence takes several seconds to read, you must be holding information for that time. Similarly, if your brain cannot store information from one visual fixation to the next, you cannot put the separate snapshots together into a whole visual scene. Finally, if you need to eat, but you can't keep your feeling of hunger in mind long enough to do something about it, you may go without food. All your sensory, motor, and cognitive functions need some immediate memory to work.

The hippocampal region continues to be an active topic of research. Because it is part of the ancient mammalian brain, it has many different functions. The surrounding medial temporal lobe is also an area of great convergence between different sense modalities.

The hippocampal regions themselves are called *paleocortex*, or "old cortex." While neocortex has six distinct cellular layers, paleocortex has four or five. In humans and other mammals, the hippocampal region is in constant dialogue with the neocortex to encode, maintain, and retrieve memories when needed.

4.0 SMALL AND LARGE MENTAL CAPACITIES

Limited-capacity processes include conscious thinking, selective attention, immediate memory, and voluntary control. *Large-capacity functions* include long-term memories, highly practiced skills, and our vocabulary. We will explore this theme next.

Even though human brains have tens of billions of neurons, in some ways they have very narrow capacities. The limits of short-term memory—the information we can mentally rehearse—is about “seven plus or minus two” separate items, as George A. Miller famously described in 1956. That number seems to apply to many kinds of unrelated items: colors, numbers, short words, musical notes, steps on a rating scale, and so on. There are only a few conditions. One is that each item must be consciously noticed for only a brief time; if it is made consciously available many times, it becomes part of long-term memory. Second, the items must be *unpredictable* from previous knowledge. If we simply ask people to remember a regular series, like 0, 5, 10, 15, 20, 25 . . . (etc.), they can keep much more information in immediate memory because they only have to remember the rule + 5. When we are prevented from mentally rehearsing items, the capacity of immediate memory drops from seven to less than four separate items (Cowan, 2001).

Selective attention is another limited-capacity function. It was initially studied using the dichotic listening paradigm (Figure 2.24). In this method, subjects wear headphones with two separate speech channels, one into each of the two ears. Subjects are asked to “shadow” one of the two channels, to repeat the incoming speech with minimum lag time. They can only hear one channel.

It is easy to demonstrate this by listening to two radio news broadcasts at the same time, for example. Under those conditions people can only understand one flow of news, though they can pick up the voice quality in the unattended channel.

For a gigantic brain, these capacity limits are tiny. Compared to a digital computer, for example, they are astonishingly small. Table 2.1 shows a dozen other phenomena that show similar, narrow-capacity limits.

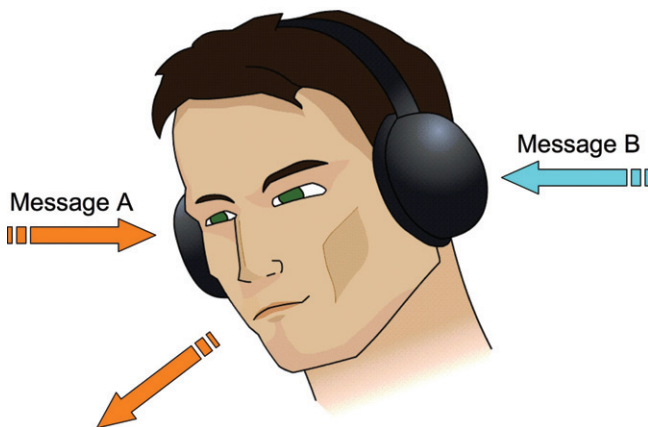


FIGURE 2.24 Selective attention. Renewed interest in selective attention emerged in the 1950s with an influential experimental program started by Donald A. Broadbent. The figure shows Broadbent’s selective listening task, in which two messages are sent simultaneously to the two separate ears. It is a classical “dual task” method for studying limited-capacity functions. Source: Baars & Fu.

TABLE 2.1 Limited-Capacity Tasks

-
1. Dual-input limits. Some 50 years of research shows that people cannot consciously understand two incompatible streams of information at the same moment.
 - a. Selective listening: receiving two streams of auditory input at the same time.
 - b. Inattention blindness: tracking two competing visual streams on a single screen.
 - c. Binocular rivalry and its variants: receiving different visual input to the two eyes.
 2. Immediate memory limits, including the capacity to hold recalled memories.
 3. Ambiguous stimuli and meanings, such as the Necker Cube, ambiguous words, and many other cases where input can be interpreted in more than one way.
 4. Competition between different features of the same object, such as the Stroop color-naming effect (see [Chapter 3](#)).
 5. Conjoined feature search: for example, searching for both color and shape in a complex display.
 6. Effortful tasks compete against each other. The more difficult two tasks are perceived to be, the more they tend to interfere. There may even be an upper bound on the number of effortful tasks one can accomplish per day (Muraven & Baumeister, 2000).
 7. Response competition. Two different output plans or actions tend to compete against each other (Pashler, 1989).
 8. Limits on temporal integration:
 - a. Attentional blink: in a rapid series of visual letters, a “blind” period may occur some 200–500 milliseconds after a target letter.
 - b. Change blindness: the difference between two visual scenes may go unnoticed if a brief white flash interrupts them. This may be a limit on the construction of coherent temporal events.
 9. Long-term memory search may be limited, as in the case of word retrieval difficulties.
 10. Conceptual incompatibility and functional fixedness. It may be difficult or impossible for people to understand an “obvious” problem from an unexpected point of view.
 11. Domain-specific limits. Specific input and output modalities may have local limitations. One example is the very small size of high-resolution vision, using the fovea. Another is our difficulty in doing certain bimanual actions, such as patting one’s head and rubbing one’s stomach at the same time.
-

4.1 Multitasking is hard—and often impossible

Personal technology has made it possible for us to try to study, listen to music, and talk on a cell phone at the same time. Sadly, our efficiency in multitasking goes down the more different things we do. We cannot do even two consciously demanding things at a time, such as carrying on a complicated conversation and driving in rush hour. If we don’t need to think much about each task, we can drive at the same time as talking, but the more conscious involvement is needed, the more the tasks will compete. For that reason, dual-task methods are often used to study how much of our limited capacity is taken up by a task. As the demands of one task rise, the efficiency of the second task will go down.

How do we deal with capacity limits? One solution is *chunking*, the ability to condense a vast amount of information into a single, organized unit. The words of natural language are often chunks: imagine the amount of information we get from words like *mother*, *school*, and *love*. We have many other ways of condensing information into single chunks. In reading this chapter, chances are that you will condense it into main points. That is a chunking strategy.

We also deal with capacity limits by using practice (Raaijmakers & Shiffrin, 1992; Chein & Schneider, 2005). A skilled video gamer may be able to talk at the same time as playing the game, while a novice must concentrate on the game. Practice is a way of lowering the capacity cost of a task. However, there is another side to this: some cognitive capacities are extremely large ([Table 2.2](#)).

TABLE 2.2 Very Large-Capacity Functions

Some brain features show massive capacity.

1. The various kinds of long-term memory.
 - a. Episodic and autobiographical memory has been estimated to be 1 billion bits (Landauer, 1986). Using recognition memory, one can retrieve old movie scenes, childhood landmarks, the faces of fellow students, and the like, dating back five decades or longer.
 - b. Semantic memory for facts and concepts is very large.
 - c. Procedural memory for highly practiced skills.
2. The language vocabulary: educated speakers of English can recognize about 100,000 words, each of which involves a complex network of related ideas, sounds, and written words.
3. The great complexity of sensory and motor processes.
4. The vast number of neurons, connections, and functional networks in the brain.

4.2 Very large capacities

The cortex is now believed to have about 1,000 functional regions (called Brodmann areas). Each patch of cortex is densely connected with all the others (see Chapter 4). The sheer amount of specialization and signal traffic in the brain is enormous, even during sleep. It is believed to rise markedly during waking and dreaming (see Chapter 8).

Our memory systems have great capacity, often so large that we do not have reliable estimates of their sizes. We can make some educated guesses. For example, the vocabulary of an educated speaker is about 100,000 words, but each word typically has more than one meaning. Further, each word enables access to knowledge domains that are far more complex than the words themselves. The knowledge we can understand and express in language must therefore be very large.

The same point applies to autobiographical memory. In a classic study, Standing (1973) showed 10,000 pictures for six seconds each to students. A week later, a sample of the 10,000 “Old” pictures were shown again, mixed with an equal number of “New” pictures. Subjects were asked to tell whether they thought the current picture was “Old” or “New.” They scored at 90 percent accuracy or above. This implies that even six seconds of conscious exposure is enough to enter a distinctive picture into long-term memory. Since human beings spend at least six seconds of their lives on their friends, their neighborhood and favorite foods, the implication is that all of those events are stored in the brain.

The challenge is not learning but retrieval. In the Standing experiment, subjects used *recognition responses*, simply looking at a picture and deciding if it was “Old” or “New.” Unfortunately, most academic exams don’t use recognition testing but recall. That is, we are given a hint and the task is to retrieve the entire memory. Recall tests are much harder. These results indicate therefore that our memory stores are very large indeed but that finding the right memory at the right moment is the big challenge. This is much like finding a book in an enormous library. If the book is filed in the wrong place, it can be lost forever. With computer-based databases, some of that work of retrieval is done for us.

Thus memory stores are a good example of very large cognitive capacities, which we often use without much effort. When you recognize a movie scene you last saw ten years ago, you are using a recognition procedure to retrieve one among thousands of movie scenes in memory. Recalling that scene based on just a cue is more difficult.

4.3 Why such small capacity limits?

The giant memory capacities shown in the functional diagram are channeled through limited-capacity systems, like selective attention, focal consciousness, working memory, and voluntary control of action. But why are those abilities so limited?

It would be nice to do half a dozen things at the same time. Why are things so limited in a brain with tens of billions of neurons? It isn't just that we have a limited capacity to *do* things—only one mouth to speak with and two hands to hold things with. Capacity limits also operate in perception, the *input* system. Ambiguous figures, like the famous Necker Reversible Cube, are very limited: we can only see one interpretation of a Necker Reversible Cube at any given moment. Most of the words of language are highly ambiguous, as we can see from the dictionary.

Some scientists believe that capacity limits are due to the role of consciousness in many specializations of a very large brain (Baars, 1988, 2002; Edelman, 1989; Llinas & Pare, 1991). Limited mental functions are closely associated with consciousness, while large-capacity functions are generally unconscious (see [Tables 2.1](#) and [2.2](#)).

5.0 SUMMARY

This chapter gave an overview of mind and brain. We now have many brain imaging studies of vision and hearing, learning and memory, conscious and unconscious processes, visual imagery and inner speech. There is a growing integration of the behavioral and brain evidence ([Table 2.3](#)). The implications are immense. This is a remarkable time of discovery. Each new finding opens up more avenues for exploration.

TABLE 2.3 Cognitive Functions in the Brain

Sensory input and sensory stores	Sensory cortex, thalamic relay nuclei
Voluntary selective attention	Prefrontal and parietal
Spontaneous selective attention	Sensory regions
Verbal WM	Broca and Wernicke's areas, prefrontal cortex, and medial temporal lobe
Visuospatial sketchpad	Visual cortex
Response output	Prefrontal and motor cortex and motor pathways
Long-term memory systems	Lasting changes in cortical connectivity

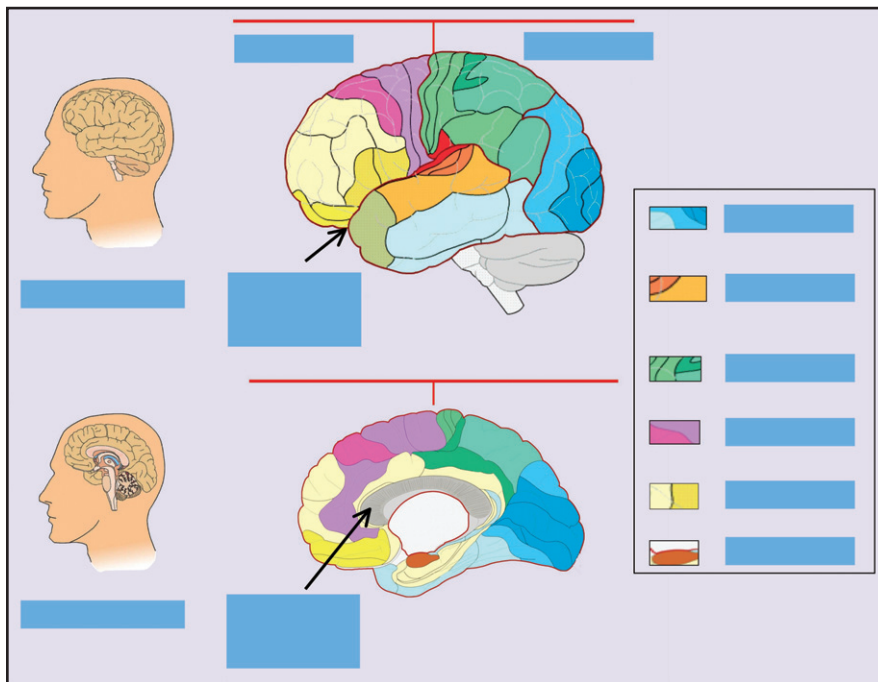


FIGURE 2.26 Label the functional regions of the brain.

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The nerve cell

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Neurons often line up in two-dimensional arrays, like flowers in a meadow. Staining techniques have been used for a century to bring out their features under the microscope. Here, layers of cortical neurons show pyramid-shaped cell bodies, with their major axons lined up vertically to connect with the next layer. The image is a computer-colored brain section, tagged with green fluorescent protein (GFP). This gives us great clarity and detail.



Source: *Brainbow*, with permission

1.0 INTRODUCTION

At first glance, the brain looks like an endlessly complicated forest of neurons. We can simplify it by understanding its basic units. Just as individual bushes and trees share a basic biological plan, so do neurons. The typical nerve cell is called the “integrate-and-fire” neuron. It is a tiny biological battery that can store electrochemical energy and discharge it by way of a fast signal going down its main output fiber.

The neuron is specialized to send signals very fast (in a few milliseconds) and very far (as far as the length of your leg, for example). Because neurons are so active, the brain uses about ten times more energy per cell than other organs.

2.0 BASIC FEATURES

2.1 Neurons and signals

We can think of animal cells in general as flexible bubbles made from fatlike molecules, floating in a watery medium, and filled with cytoplasm—a complex mix of water, organic molecules, microthin fibers and organelles, and a central nucleus with DNA.

Neurons are similar to other animal cells, but their shape differs in one major way: they have specialized branches for signal input and output. *Dendrites* (*input fibers*) and *axons* (*output fibers*) are thin micron-sized tubes extruding from the cell body; a neuron may have ten thousand input branches and one or more output fibers. Figure 3.1 shows a simplified neuron.

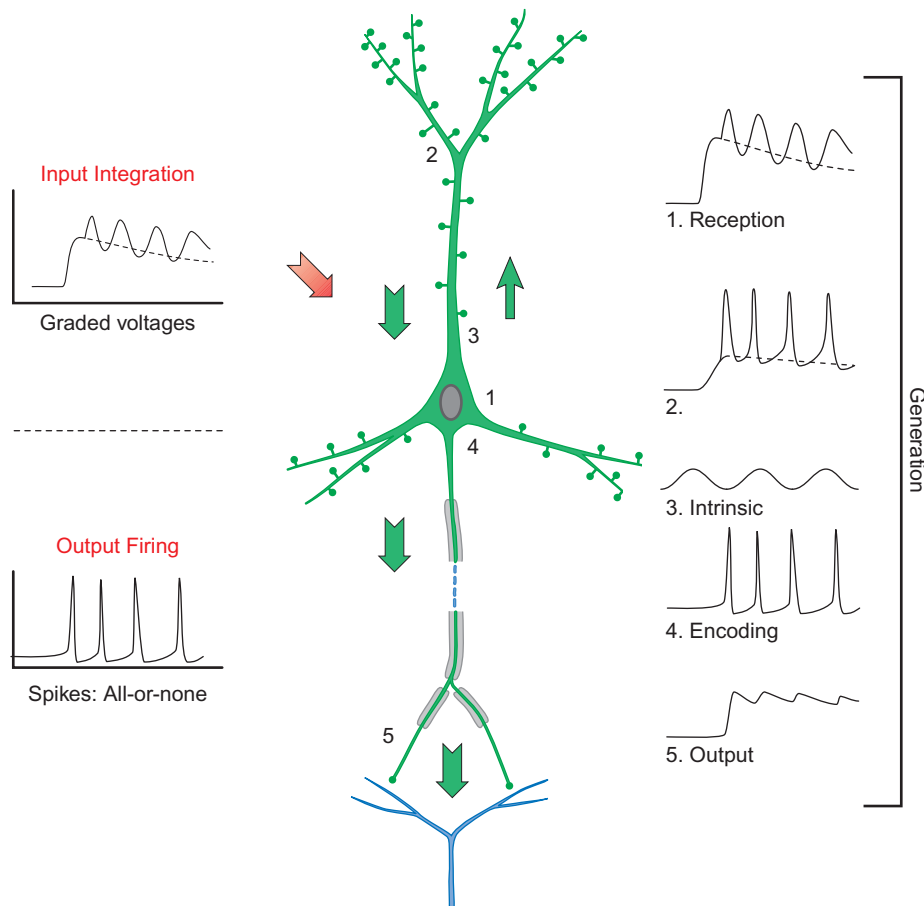


FIGURE 3.1 The integrate-and-fire neuron. A neuron with its dendrites on top, showing their spines as tiny knobs. Dendrites receive synaptic inputs that evoke graded membrane potentials (labeled in red as Input Integration). When dendritic potentials rise above the threshold in a very brief time interval and are added to the intrinsic membrane potentials, they can trigger an all-or-none spike (Encoding). Spikes cause the release of neurochemicals at the synapse. These can start the whole process again in the next neuron. Source: *Modified from Byrne & Roberts, 2004.*

2.2 The integrate-and-fire neuron

We can compare a neuron to an archer's bow and arrow. Pulling a bowstring with an arrow takes a lot of physical energy. We can do that gradually so that over five seconds we may just pull the bowstring away from the bow. As long as we exert a strong pull on the string, we are keeping energy stored in the bent bow and string. But as soon as we release the string, the energy suddenly discharges by accelerating the arrow toward the target. The physics of batteries, neurons, and archery are similar.

When a neuronal discharge reaches the end of an axon—the long output fiber—it triggers the release of signaling molecules that are recognized by the next cell, which starts the process all over again. The ability to take in stimuli from many cells and add them up in a gradual way is called *integration*. It is often useful to integrate inputs from a lot of cells in a single cell. The discharge of the membrane voltage via a fast spike (or action potential) traveling down the axon is called the *firing* of the neuron.

The standard nerve cell is therefore called the *integrate-and-fire* neuron. Like other living cells, neurons carry their own molecular machinery, and like an electrical battery, neurons store energy.

Neurons convert their *membrane charge* into fast signals. When the neuron receives signals from other neurons, its membrane voltage starts to change gradually until it rises past a threshold, about -55 mV. That causes the ions on both sides to try to equilibrate by rushing to the other side of the membrane for about a 1 millisecond. As the charge breaks down in one small region of the membrane after another, the all-or-none spike fires down the output branch.

When the spike reaches the endpoints of the axon, the cell releases signaling molecules called neurotransmitters. These diffuse across the tiny synapse to trigger receptors on the next neuron, which starts the process all over again.

Nerve cells may fire their spikes up to several hundred Hz, much more slowly than the electronic chips that run computers. The brain has many more neurons than a standard computer has central processing chips. Brains still do many things far better than current computers. Computers do not reach human performance at this time in terms of perception, language, semantic understanding, action control, or artistic creativity. Brains are often called “massively parallel” biocomputers, like very large sets of digital computers. The cortex plus the thalamus is more properly called a *parallel-interactive* society of computers, comparable to the World Wide Web, where any computer can communicate with many others, and vice versa. (See [Chapter 8](#).) [Figure 3.2](#) shows how the membrane stores energy.

Like a cell phone battery, a cell membrane stores potential energy by separating positively and negatively charged particles. Your cell phone battery is charged by your local power grid, which is supplied from power generators run by fuels like coal or natural gas. Biological batteries obtain their energy from food and oxygen. The brain is the most energy-intensive organ in the body, and it demands the fastest food, which is glucose (a kind of sugar), plus oxygen from the lungs.

Each body cell contains numerous smaller cells called mitochondria, which convert glucose and oxygen into a huge variety of activities in the cell. We will focus on only one kind of protein activity called “ion pumping.” Ions are charged particles. When crystalline molecules like salt (NaCl) are dissolved in water, they tend to drift apart into two ions: Na^+ and Cl^- . Since all body cells are bathed in a watery medium, both inside and outside the cells, simple molecules easily drift apart into their component ions. The long organic proteins that make up cellular structures like DNA are much more stable and long-lasting than simple molecules like table salt.

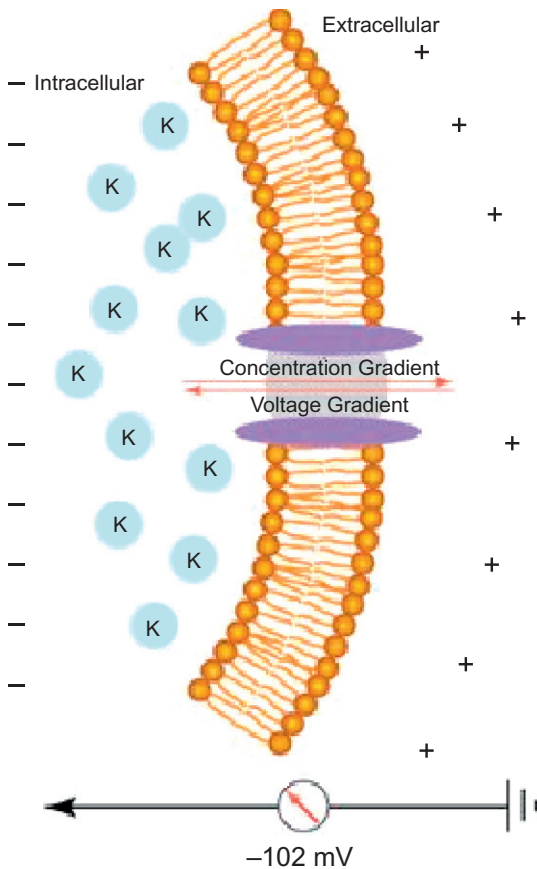


FIGURE 3.2 The neuron's membrane stores electrical potential. The two-layered membrane is both flexible and lasting, and it allows smaller molecules to filter through. Large molecules are generally kept on one side of the membrane. Source: McCormick, in Byrne & Roberts, 2009.

Ion pumps are tiny protein machines that are embedded in the membrane of each cell. They pump negative ions to the inside of the cell and positive ions to the outside. The positive ions include potassium (K^+) and calcium (Ca^{+2}) and the negative ones include chloride (Cl^{-2}).

The result is a polarized biological battery—one that keeps a swarm of negative ions on the outside and positive ones on the inside. The result is a voltage gradient of -70 millivolts (mV), negative on the inside and positive on the outside.

The cell membrane is a remarkable biological structure. Imagine putting a few drops of a soaplike liquid into water and watching tiny bubbles emerge. These bubbles are long-lasting and flexible, made of “bilayer lipid” membranes, two-molecule-thick skins. “Bi-lipid” means two lipid (fatlike) molecules, which have the useful property that one end is attracted to water, while the other end is repelled by water. All the hydrophilic (water-loving) ends line up, pointing to the watery medium around or inside the cell. The hydrophobic (water-fearing) ends point to each other to avoid contact with the water. The resulting two-layered membrane is both flexible and lasting, and it allows smaller molecules to filter through. Large molecules are generally kept on one side of the membrane.

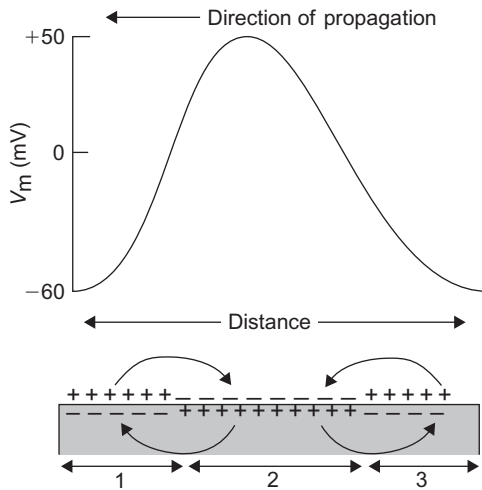


FIGURE 3.3 Spikes run down the axonal membrane. Neuronal signals travel along axons through the exchange of positive and negative ions in adjacent regions of membrane. In the axon, region 2 is undergoing depolarization, while region 3 has already generated the action potential and is now hyperpolarized. The action potential or spike will propagate further by depolarizing region 1. Source: *Ramachandran, 2002*.

In addition, ion pumps are embedded in the membrane; some of the ion pumps pump molecules to the inside of the membrane, and others to the outside. The cell membrane is a good example of spontaneous self-organization in nature (Figure 3.3).

2.3 Spiking codes

Most individual neurons fire between 10 and 100 Hz (Figure 3.4). The lower number is typical for a neuron in the cortex that is not receiving direct stimulation. Different spiking codes can code for stimulus intensity and quality in perception and learning (Figure 3.5). After hundreds of millions of years of evolution, the brain has evolved many different neurons with different temporal and spatial codes.

Neurons in the basilar membrane of the inner ear can fire quite slowly, when the eardrum vibrates to low sound frequencies. The auditory nerve can fire much faster, but that is as a *bundle* of neurons, not a single one. The individual neurons in the auditory nerve take turns sending out spikes, and the large bundle of auditory neurons together can follow the vibrations of the eardrum up to 800 to 900 Hz.

When a microelectrode is inserted in a single cell, it can record “intracellularly” compared to a reference level outside of the cell (Figure 3.6). Another useful approach is to locate a microelectrode *outside* of nerve cells in order to pick up the electrical field that is generated by each neuron. The EEG is a massive electrical field that may be recorded from the scalp or from the surface of the cortex. Scalp EEG mostly reflects the dendrites of pyramidal neurons (with pyramid-shaped bodies) that point their axons inward to the center of the brain. The dendritic voltages are closely correlated with the firing of the cell.

Unfortunately, scalp EEG, which is the cheapest and least invasive technique, also cuts down the electrical field signal by a factor of about 1,000. Therefore, 99.9 percent of the

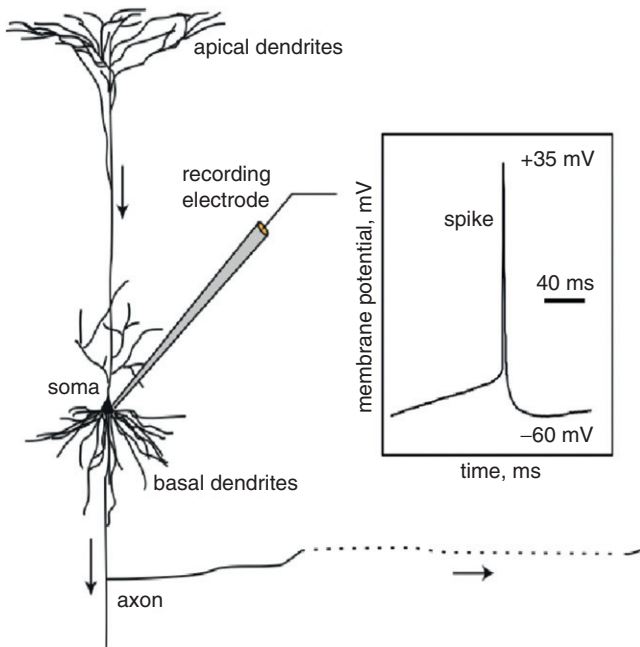


FIGURE 3.4 Recording neuronal activity. A microelectrode can be inserted anywhere in the neuron. Dendritic (input) voltages are gradual rather than all-or-none. But recording immediately after the cell body (soma), the microelectrode records classical spikes from the long output fiber, the axon. In this figure we can only see a small part of the axon, which can extend the length of the brain. Notice that the baseline voltage is -60 mV and that the spike peaks only for a few milliseconds in any part of the axon. Membrane proteins start pumping ions very fast in order to restore the baseline voltage.

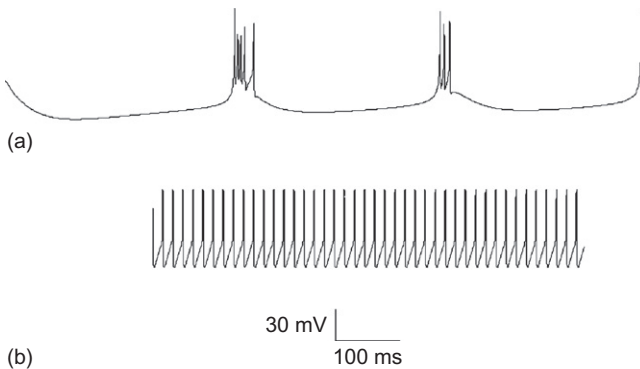


FIGURE 3.5 A neuron with two firing modes. These spike firing patterns were observed in a single neuron located in the thalamus of a cat. This neuron fires differently in the waking state than in deep sleep. Which firing mode do you think occurs during waking? Which happens during sleep? Source: Sanchez-Vives & McCormick, 2000.

electrical energy from the cortex is lost because layers of skin, scalp, and other tissues reduce the electromagnetic field strength.

Microelectrodes in brain tissue can *stimulate* neurons electrically, as well as record from them (Figure 3.7). This fact is sometimes used in brain operations that are designed to change some small region of the brain that is believed to be pathogenic—to cause serious illness. Thus it is possible to stimulate a very precisely defined brain region or to kill a small clump of neurons that may be doing harm. Drugs can also be administered very locally. Current medical research shows promise for deep brain surgery in incurable depression. It has been used to resolve epileptic conditions for the past 60 years.

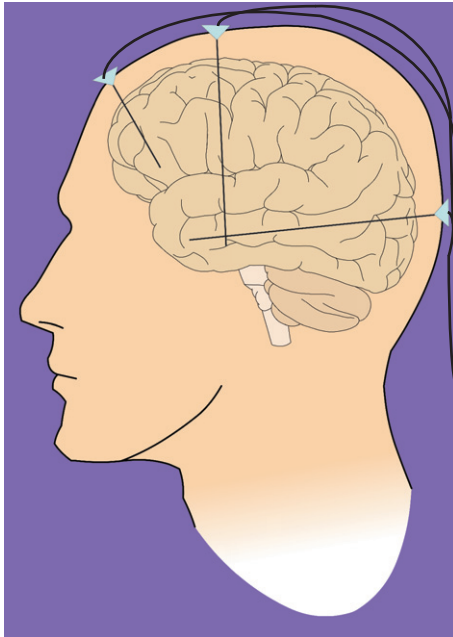


FIGURE 3.6 Single neuron recording deep in the brain. For some medical conditions it is vital to record from single neurons in the human brain. This figure shows how electrodes may be inserted horizontally from the back of the head, vertically from the top, and diagonally through the frontal scalp. Small holes are drilled under local anesthesia in the layers of outer tissue and can even be glued into place to record over a period of hours or days. As the microelectrode travels inward, the surgeon monitors the firing pattern of each neuron that is pierced until the desired cells are reached. Simultaneous x-rays are taken, superimposed on an MRI map of the patient's brain, to help guide the ultrathin electrode to the right region. In the case of epilepsy, for example, the temporal lobe is a common focus of scarring that can trigger serious seizures. Notice that two of the inserted electrodes cross over in the temporal lobe. Source: *Baars & Fu with permission.*

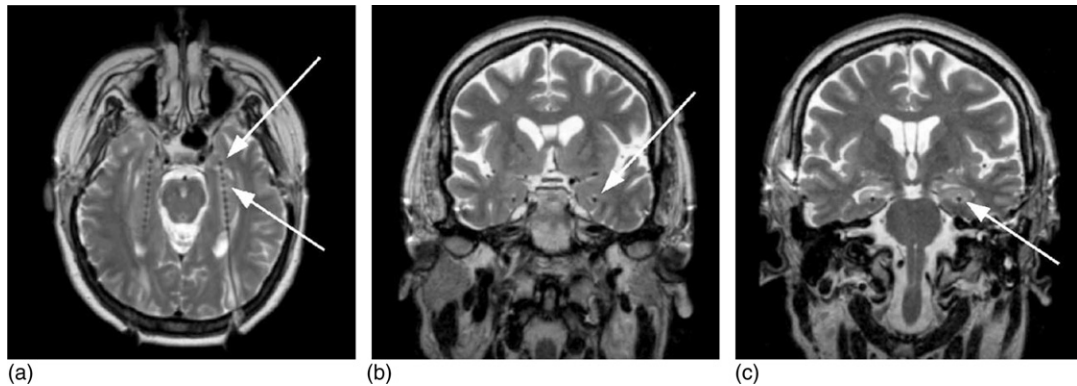


FIGURE 3.7 Depth electrodes in humans. Structural scans of one horizontal and two coronal slices of the living brain. While most single-cell recording is done in animals, human studies have been done when depth electrode recording is medically necessary. The arrows point to electrode placements in the temporal lobe. If you look carefully at the left MRI scan (a), you can see two electrode tracks and two small holes in the rear of the scalp through which they were inserted. Neurosurgery like this is generally safe and painless because the brain itself does not contain pain-sensing neurons. In scan (c) you can see the brainstem (dark gray), indicating that the coronal section is taken above the brainstem at the back of the brain. Source: *Dietl et al., 2005.*

2.3.1 The synapse

Many neurons communicate by chemical synapses. The neurons in [Figure 3.8](#) are intertwined with one another and show several kinds of synapses. Almost all of the chemicals that affect the brain act on specific synapses, including coffee, chocolate, alcohol, medications, and the like.

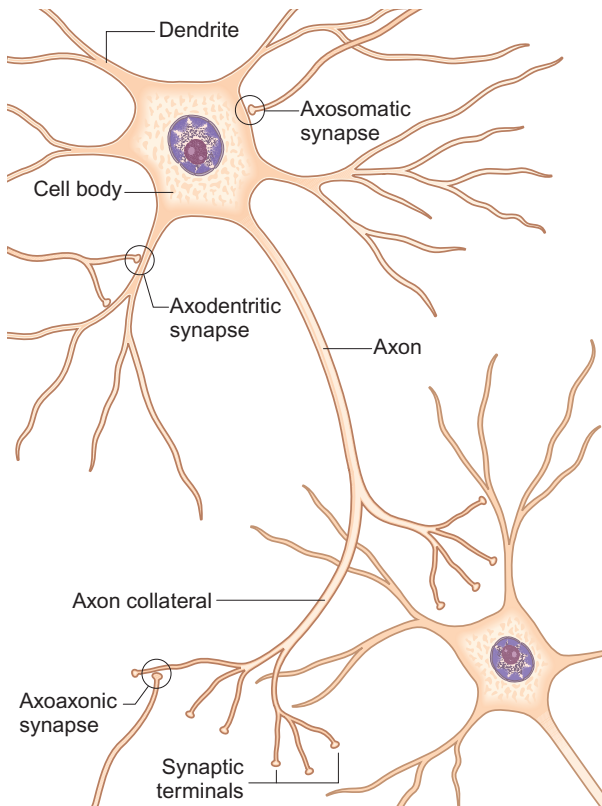


FIGURE 3.8 Neurons are connected through synapses, which can be excitatory or inhibitory. The probability that the next neuron will fire a spike is increased if it is an excitatory connection and decreased if it is an inhibitory connection. Source: Byrne and Roberts, 2009.

Most functional networks in the brain use both excitatory and inhibitory neurons. When excitatory and inhibitory neurons interact, we commonly see *oscillations*. The alpha rhythm is an example of an oscillation we can see in the occipital EEG when people close their eyes.

Classical neurons are connected by way of synapses (see [Figure 3.8](#)), which can be *excitatory* or *inhibitory*. Excitatory synapses increase the chances that the next neuron will fire, while inhibitory ones decrease the next neuron's activity.

A neuron may have ten thousand input synapses and a dozen output synapses terminating on other neurons. Many other factors determine the activities of neurons: the sleep-waking cycle, the availability of chemicals for making neurotransmitters, and more. These factors all affect the likelihood of a signal going between two neurons.

The great variety of neurons can be simplified into an idealized neuron—the integrate-and-fire unit—and the many ways in which neurons can trigger each other can be simplified into connection probabilities between neurons.

2.3.2 Synapses as stop/go switches

Why does neuronal signaling require so many steps? Why not just glue all the nerve cells together to make up one long, continuous wire, like an electrical circuit? In fact, there are nerve cells that touch each other directly, without a synapse.

A major reason for the chemical synapse is to allow neurons to act like switches, like the transistors that make up a computer chip. Figures 3.9 and 3.10 show detailed views of the synapse. Some neurons release the amino acid glutamate. Others release the amino acid GABA (gamma amino butyric acid). The first molecule is excitatory; it tells the receiving cell to go faster. The second one is inhibitory; it tells the receiving cell to slow down. These two molecules are the most common neurotransmitters in the cortex—the outer shell of the brain. You can think of the excitatory/inhibitory difference as a traffic signal switching from green to red, permitting a flow of traffic or stopping it. The synapse is the place where a “Go” versus “Don’t go” signal can change the activity of the target cell. Figure 3.11 shows different types of neurons. Interestingly, GABA tends to increase during sleep, and sleep medications often increase GABA in the brain.

Another reason for very local synaptic signaling is to control the number of molecules that are released. Glutamate can combine with other molecules to become toxic, killing nerve cells. Therefore, another reason for a very precise, very localized squirt of glutamate into a synapse is to clear toxic by-products as quickly as possible—within milliseconds.

All physiological organs maintain optimal levels of activity, neither too much nor too little. The body maintains delicate control over blood pressure, body temperature, the amount of oxygen in the bloodstream, glucose concentration, food intake and energy expenditure, acidity, and hundreds of other variables. Having different neurotransmitter chemicals like glutamate and GABA is also a way for the brain to regulate its own activity level. If the cortex becomes too active, a little more GABA can bring it back to the optimal level of functioning. If you are feeling sleepy and unable to concentrate, an increased level of glutamate might make you feel more alert.

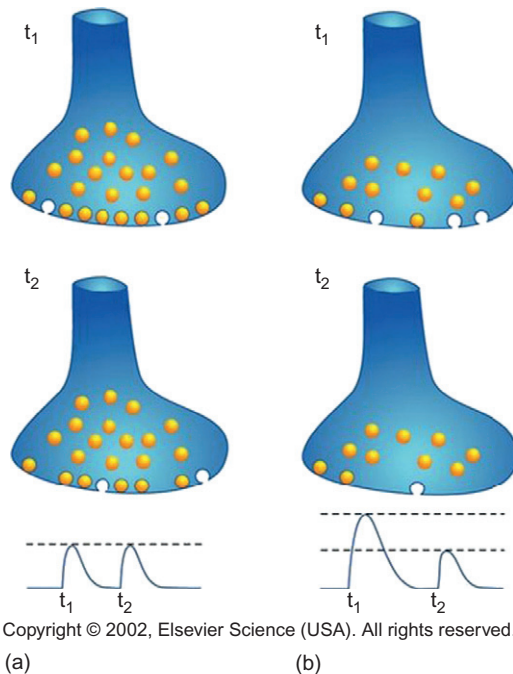


FIGURE 3.9 A simplified image of the release of neurotransmitter molecules from vesicles (yellow bubbles) that transport the molecules from their site of manufacture, which may be in or near the nucleus, or in other organelles inside of the presynaptic neuron. Vesicles flow in a regulated sequence, often guided by microtubules, essentially submicroscopic tubes inside of the axon. On the left (a), the flow of vesicles leads to release of transmitter molecules in two equal bursts. In (b), the first burst depletes the terminal button, so that the second release is decreased.

Terminal buttons release neurochemicals into the synapse. Source: Schwarz, in Squire et al., 2002.

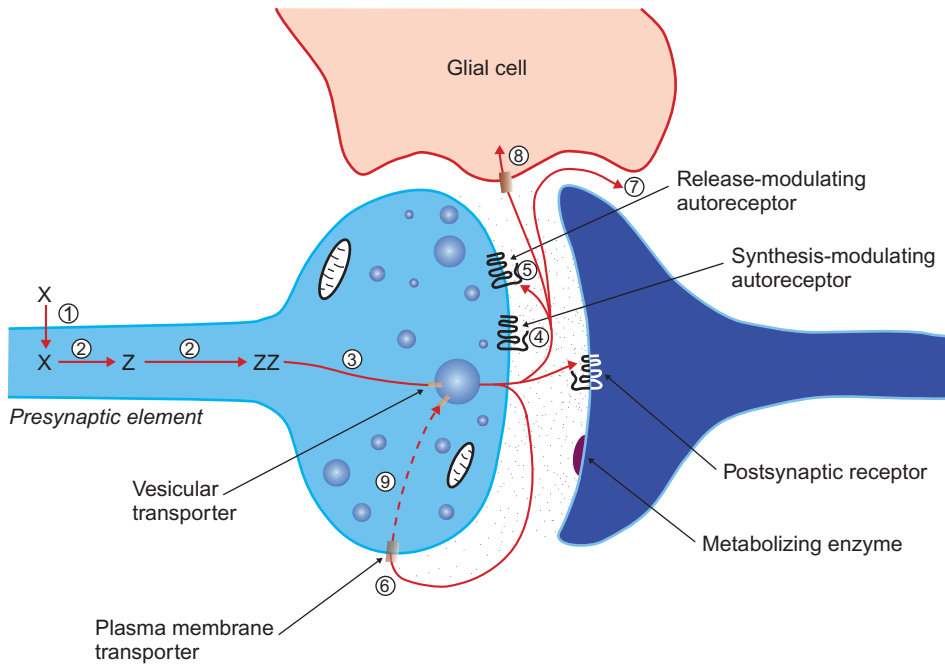


FIGURE 3.10 A basic synapse. The *presynaptic* cell triggers *postsynaptic* changes. Two cells in contact are labeled pre-synaptic (the lighter blue) and postsynaptic (darker blue). A spike in the presynaptic cell triggers the release of a chemical neurotransmitter that diffuses across the synapse and lowers the membrane potential of the postsynaptic cell. Source: *Standring, 2005*.

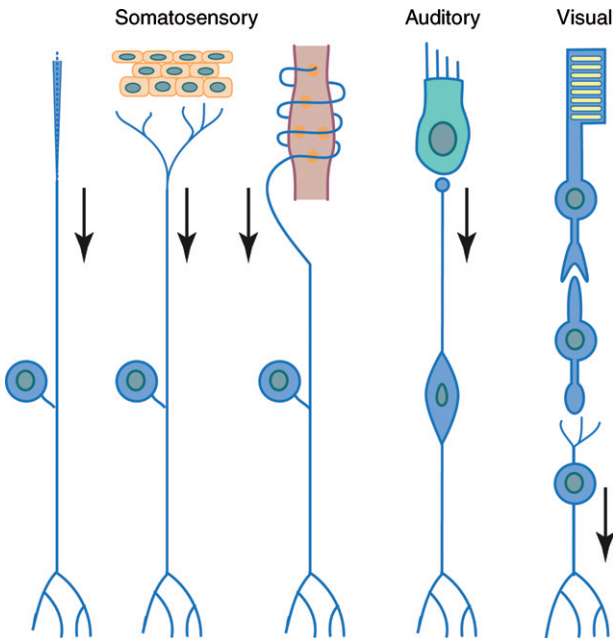


FIGURE 3.11 Sensory receptors convert outside energy into neuronal activity. Different sensory receptors pick up different kinds of energy, like light (the eyes), air vibrations (the ears), mechanical friction (touch), and molecular signals (taste and smell), and convert them into neuronal messages. Thus all the sensory receptors are modified neurons. Source: *Squire et al., 2002*.

3.0 HOW NEURONS COMBINE

Neurons cluster together in simple ways. In practice, neurons that perform actual tasks involve combinations of these clumps. To use the forest analogy, our brain forest, which looks so complicated at first, has many meadows with grass and flowers, which are nearly flat arrays of light-sensitive surfaces. This allows us to look at the forest in terms of bushy neurons with many roots and branches and nearly flat meadows strewn with grass and flowers, which all need to get the most sun exposure they can. Even the streams of water that feed the forest have a brain analogy because the brain receives a rich supply of nutrients from the bloodstream and from its internal fluid supply.

Neurons commonly combine into chains of neurons, bundles, small circuits, flat arrays of neurons, and linked arrays, called *hierarchies*. In *chains of neurons*, each nerve cell triggers another one. Spinal reflexes are often shown as such chains (Abeles & Gat, 2001). The major sensory nerves are excellent examples of giant bundles of neuronal fibers. The optic nerve is a bundle of about 1 million axons coming from the ganglion cells of the retina and wrapped in a strong, protective sheath. Seen with the naked eye, the optic nerve looks like a whitish wire, a few millimeters thick. Such large bundles of fibers make up the signaling highways of the nervous system. The “white matter” of the cortex mostly consists of such bundles.

The *small circuits* are like spinal reflexes and are the minicolumns of the cortex (Figures 3.12 and 3.13). Neurons can also make up simple circuits, like the knee-jerk reflex. The figure at the beginning of this chapter shows *flat arrays* of neurons. The retina is a beautiful example of a flat array of receptors, and the biological reason for that is clear: it’s why flowers spread out over a flat meadow and turn their petals to the sun, to absorb the greatest amount of light. The light receptors in the retina do the same thing. Chapter 1 also showed the example of the compound eyes of the fruit fly, which are also arrays. The retinal array was discovered by Ramon Y Cajal, often considered to be the founder of neuroscience.

Video cameras and screens also use flat arrays of sensors or light-emitting pixels. Some biological principles are so basic that they show up in many different species. Human beings often discover the same principles that nature found long before.

Linked arrays are called *hierarchies*. Some brain arrays are point-to-point mirror images of others. For example, the receptors of the retina are echoed point-to-point in the thalamus, where the optic nerve stops and is relayed to the next map. Even the first visual map in the cortex, called V1, is a close copy of the retina. Much of the cortex can be viewed as *topographical* maps, flat patches of neurons that preserve spatial relationships from other flat patches.

However, higher-level visual maps are *not* copies of the input. They are fuzzier and more abstract maps, taking the input apart into features like color, motion, size, and object identity, and then putting them together into coherent conscious objects and events. What people report about their sensory experiences is the *conscious* result of a largely *unconscious* set of neural maps, which bounce signals back and forth until they settle on the best interpretation of the input. (See Chapter 8.)

Figure 3.14 shows how visual maps (arrays) with similar topographies are combined in a hierarchy of maps. We will see in the chapters on hearing and vision that sensory systems have arrays of *higher-level features* as well, like color, motion, size, and shape. Looking at a

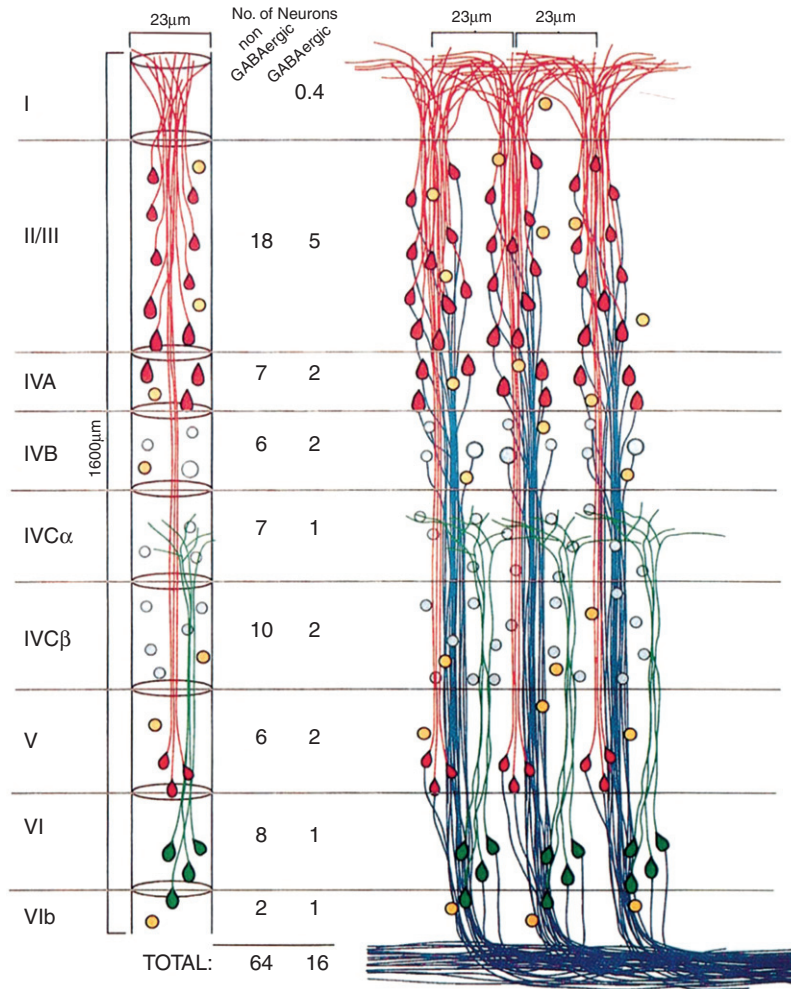


FIGURE 3.12 Cortical columns—basic circuits of the mind. Long pyramidal neurons in each column stand out very clearly. Each long (pyramidal) neuron is surrounded by *inhibitory interneurons*, which help to stabilize the output of the excitatory cells. Notice the layer numbers on the left side, which are based on the microscopic cellular patterns of the cortex. Cortical layers are remarkably stable in the very large area of the “neo” cortex (the mammalian cortex). Source: Mountcastle, 1997.

coffee cup involves a pixel map on the retina. Higher up that becomes a color map, a motion map (if you jiggle the cup), and an object map. Those abstract maps correspond topographically to pixel-level maps like the retina, but their cells represent abstract features rather than single points of light.

As we will see later, the cortex is a six-layered sandwich of linked arrays. [Chapter 4](#) shows how the cortex can be mathematically flattened into a sheet about the size of a dinner napkin.

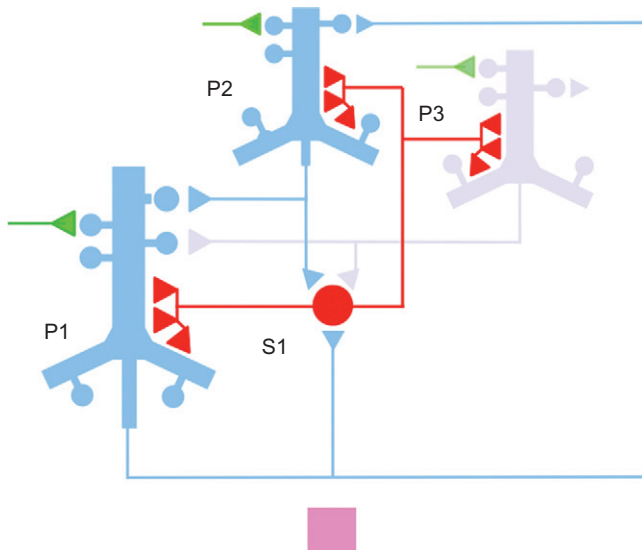


FIGURE 3.13 All cortical circuits involve both excitatory and inhibitory neurons. The pyramidal cells of the cortex are shown in light blue, and the inhibitory interneurons in red. Green neurons coming from outside of the system (perhaps from the visual tract) drive all the cortical pyramidal neurons. S1 refers to 'smooth' neurons, which are also excitatory. Microcircuits like this are pervasive in the cortex, and make for local differences between anatomically similar regions of the brain. Source: *Douglas and Martin, 2009*.

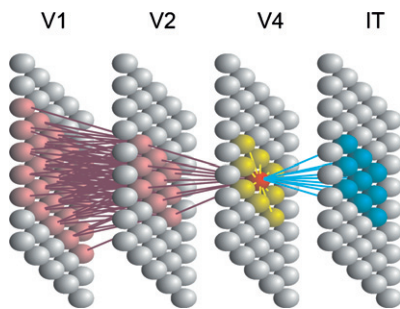


FIGURE 3.14 The visual cortex is a set of maps. The beginning of the visual pathway in the cortex consists of topographical or visuotopical maps that work in registration with each other. Thus the center of the visual array in each map must correspond well to the center of the array in the next map, and so on. Later on, visual maps become more complex because they must explain more abstract aspects of the visual world that are not necessarily locked to a specific retinal location

When we look at the electrical activity of tens of billions of neurons, the entire brain seems more like a symphony orchestra than like a single piccolo.

While reflex circuits can be triggered by outside stimuli, they are normally integrated seamlessly into voluntary, goal-directed activities (Figure 3.15). For example, you can turn your head from side to side while reading this sentence. That is, you can follow a voluntary goal (stated in the previous sentence), and your oculomotor system will still keep your eyes focused on the moving window of the words you are reading at this instant in time. It is a remarkable achievement of sensorimotor adaptation, and most of the time it is quite unconscious and automatic. Oculomotor coordination is not just a simple reflex arc.

Voluntary brain mechanisms, guided by explicit goals, are controlled by the cortex in humans. Very sophisticated subcortical circuitry is also engaged in planning and executing

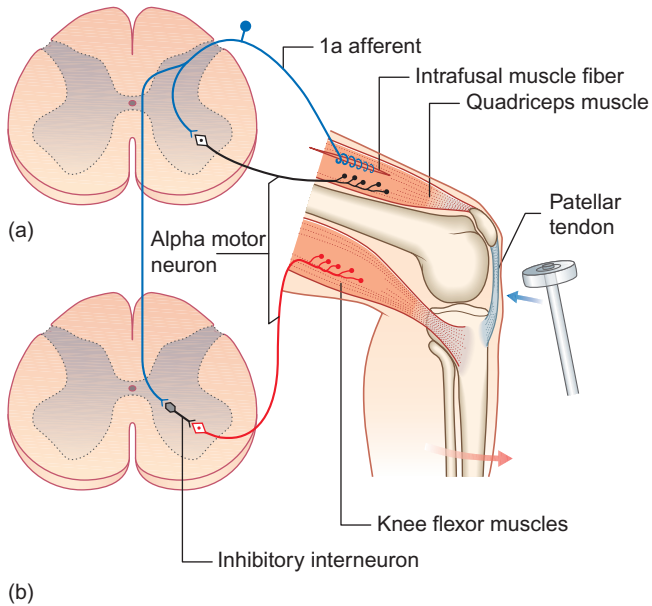


FIGURE 3.15 A simple reflex circuit. If you drape one leg over the other and tap just below the kneecap, your lower leg will jump out. This is the famous knee-jerk reflex. It is a classical example of a spinal reflex, controlled by a simple circuit. Sensory neurons pick up the mechanical tap, and transform it into a neural signal which is sent to the spinal cord. There, an interneuron links the sensory impulses to motor neurons, which contract the muscles in the upper thigh, making the lower leg jump outward. The spinal reflex as a small circuit. Source: *Standring, 2005*.

actions. Spinal centers may carry out commands from higher centers using sensorimotor reflexes, but they also return feedback signals to the brain. All these levels of control have *endogenous* (internal) as well as *exogenous* (sensory) input, both conscious and unconscious (Goodale & Milner, 1992). Thus, while there are certainly some simple reflex circuits like the famous knee-jerk reflex in Figure 3.15, reflexes rarely work in isolation. They normally work in the service of cortical goals.

3.1 Receptors, pathways, and circuits

Figure 3.6 showed an example of a single neuron in the thalamus, which shows two different spiking patterns. The timing of a neuronal spike relative to other neurons can also convey information, much as a clock shows the time of the present moment relative to the 24-hour cycle. When two neurons or neuronal populations generate waveforms, they can be *synchronized* or *phase-locked* to each other. Recent findings show that some neurons can determine their own phase-lag relative to some large populations of neurons that may generate theta waves, for example (4–7 Hz). Thus theta and alpha waves may operate like a system clock in a computer, and widely scattered neurons may be able to tune into the dominant brain rhythms to coordinate their own activities. Theta or alpha populations may serve as pacemakers for large populations of cortical neurons.

Current evidence shows that in addition to spatial coding (using sensory or motor arrays, for example), the brain also uses temporal codes (in which individual neurons fire in relationship to some dominant rhythm, such as theta and alpha).

3.2 Maps

As just mentioned, the sensory surfaces of the nervous system are flat arrays of neurons, comparable to a field of grass or flowers. Plants spread out horizontally to maximize the amount of sunlight that can reach each green leaf. Neurons use the same strategy for slightly different reasons. But in the case of the retina, for example, light receptors also need to maximize their exposure to incoming light. Arrays and “maps” (topologically organized arrays) are extremely common in the brain, and some scientists believe that the entire brain can be considered as one gigantic array of neurons (Figure 3.16).

It is therefore attractive to show the visual cortex, for example, as a series of two-dimensional arrays, starting with area V1 (the first place where the optic nerve reaches the cortex). Each successive visual array is specialized to select certain features of the visual input, including “pixels” (small differences of light and dark), size, color, motion, shape, and, higher up in the hierarchy, also entire scenes. The attractive analogy is to a set of video cameras, each one with its own array of light-sensitive elements and feeding into one another in a point-to-point fashion. Thus the center of the array is the same, regardless of what level of analysis is involved.

Such analogies are attractive but not necessarily entirely correct, so we have to be careful in using them. For example, while the retina, the visual thalamus, and V1 all involve tiny, high-resolution spatial arrays, the higher visual maps become less detailed as they start to represent more abstract objects and events. The eyes are also in constant motion, and the visual system must somehow extract stable visual information from very jumpy eyes. Thus the visual representation of the world must become independent of the specific moment-to-moment visual input in the brain. Humans and animals are also in constant motion—our heads move as well—and when we are babies, we are even carried from place to place. All those conditions change what the retina takes in, but the visual brain must still maintain a stable understanding of the visual world. Figure 3.17 shows how the visual system “maps” the input. The idea of the senses like vision consisting of “maps” of the retinal input is therefore attractive, and partly true, but it cannot explain the higher levels of the sensory pathway in the cortex. In vision, touch, and muscle control, arrays of neurons are topographically arranged as “maps” of the spatial surroundings.

Layered hierarchies are not rigid, one-way pathways. They allow signals to flow upward, downward, and laterally. A major function of the downward flow of information in the sensory systems is the need to resolve ambiguities in the input. Ambiguities are common in visual scenes but also in language and the other senses. In motor systems, upward (bottom-up) flow of information is similarly useful to help make choices in output plans and motor commands.

FIGURE 3.16 Neurons self-organize into layered arrays and circuits. What looks like a grass field actually consists of thousands of pyramid-shaped neurons, made visible by green fluorescent protein. The brain has thousands of such arrays. Nerve cells line up next to one another to create a flat array. Under the right conditions, neural progenitor cells turn into “layer cakes” (layered arrays) and circuits of mature neurons. The microscopic photos here show neuron arrays in the process of formation (a–d). Photos (e) and (f) show circuits in the process of formation. Unlike human-made computers, neurons don’t need an external hardware engineer or software programmer. They “self-organize” during gestation and are then selected, strengthened, and pruned by the life experiences of the organism. Source: *From Brainbow, Center for Brain Science, cbs.fas.harvard.edu* Pyramidal neurons in the dentate gyrus of the hippocampus. Individual neurons are brought out using a green fluorescent protein technique.

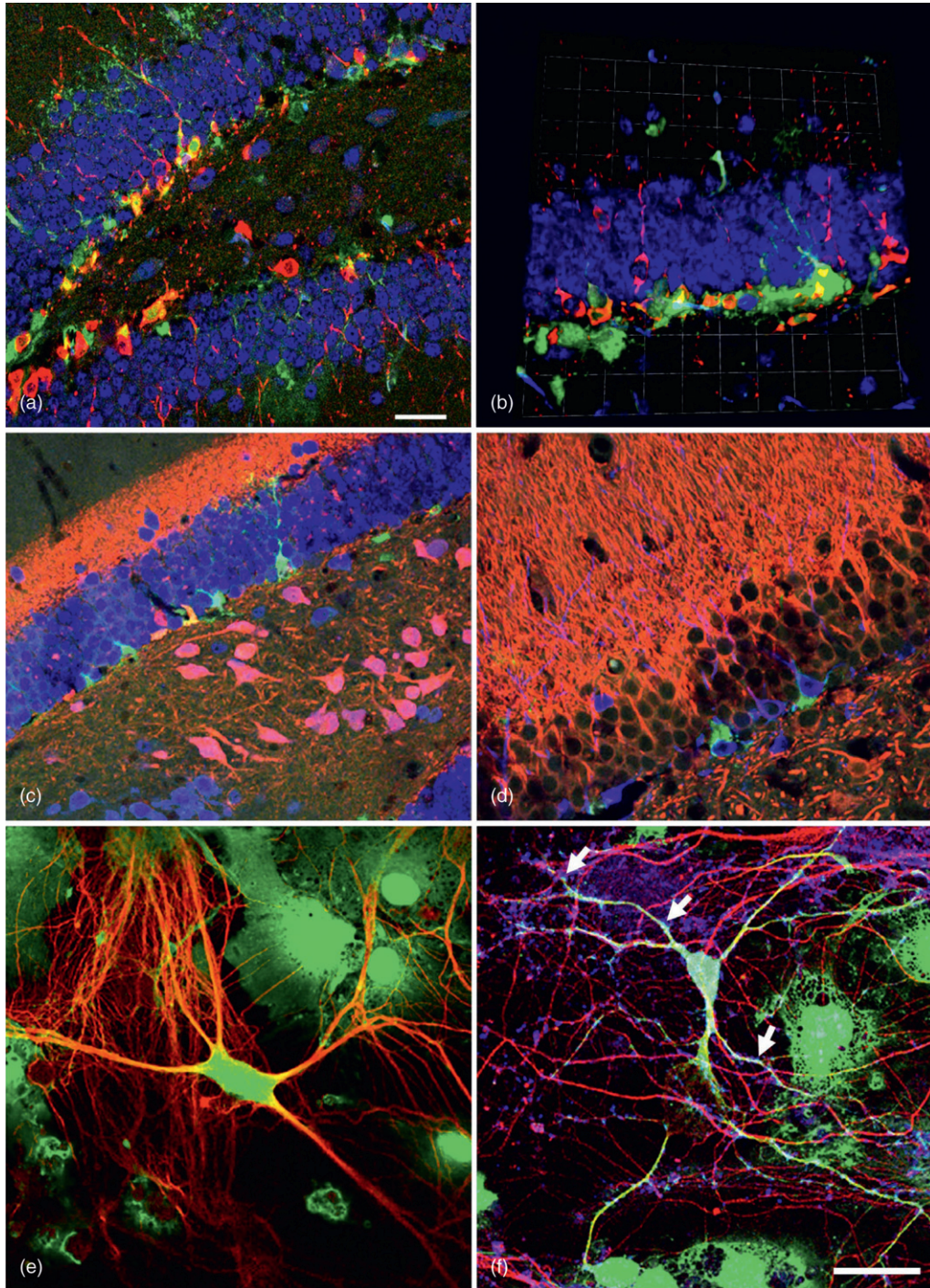


FIGURE 3.16 See figure legend on opposite page.

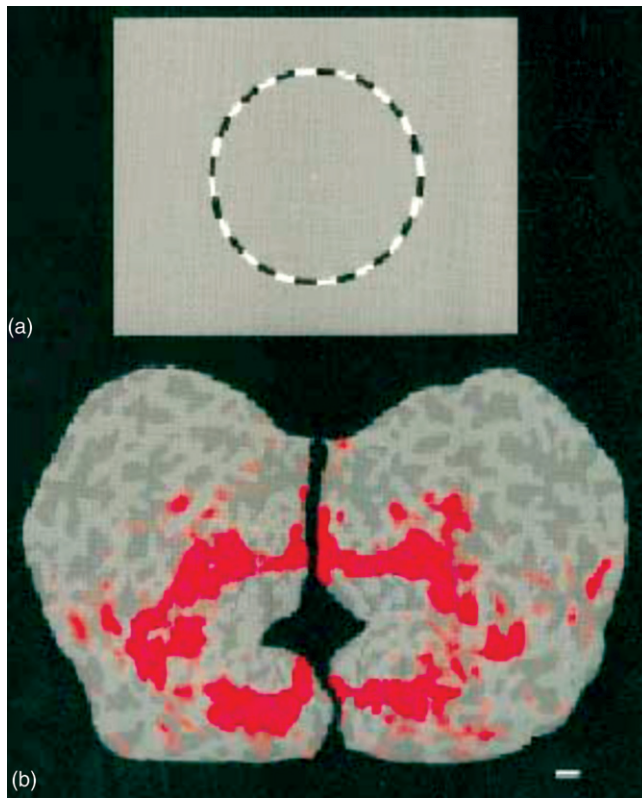


FIGURE 3.17 A visual light circle is echoed by a circular pattern of brain activity in the occipital cortex.

Lateral inhibition is a strategy for emphasizing differences between inputs, like two neighboring patches of light and dark. Cells in the sensory systems have receptive fields that are attuned to specific types of input, such as line orientation, color, movement, shape, and object identity.

As the visual maps go deeper into the cortex, their spatial resolution becomes less, but their ability to integrate large amounts of information goes up. While we study the sensory and motor systems separately, the brain is a giant sensorimotor engine, which allows constant interaction of input and output at all higher levels.

Arrays of neurons support *spatial* coding of information, but there is temporal coding as well. The regular rhythms of EEG are believed to reflect massive coordinated activities among large populations of neurons. Recent research suggests that gamma activity may be involved in such processes as sensory integration into conscious percepts, and theta has been associated with retrieval from long-term memory.

The body senses, like touch and pain perception, also project to maplike regions of the cortex. Other senses, like hearing, smell, and taste, are less spatial in nature, but the auditory cortex has maplike regions organized by pitch, like the strings of a harp. Thus, even the non-spatial senses show regular neuronal arrays and maplike regions. Finally, information from specific sensory systems is combined in the parietal cortex, using spatial arrays that combine

auditory, visual, and touch information into maplike regions. These include a body-centered map (called egocentric) and an object-centered spatial array (called allocentric). It seems as if our brains like to organize a vast amount of incoming information in arrays that mirror the layout of the spatial surroundings. And motor cortex, as you might guess, looks much like a distorted map of the output systems, the skeletal muscles of the body.

It is tempting to think that with the sensory half of the cortex (the posterior half) using so many maps, there must be a little person inside looking at the maps. But this is the “homunculus fallacy,” as philosophers call it. The trouble with this idea is that it explains nothing but merely moves the question to another level: Does the homunculus have its own brain, with its own spatial maps, and another, even tinier homunculus sitting inside?

The question for scientists is therefore how to make sense of the great number of spatial and other neuronal arrays in the brain without resorting to the fallacy of supposing that we all have a little creature inside who is looking at all the neuronal maps. Neural network models provide one set of answers today, as we will see.

Although there are some one-way streets in the nervous system, as we go higher up, almost all neural pathways turn out to involve *two-way* connections (Figure 3.18). This is an important principle of the brain that has been called *reentry*. In the auditory system, for example, the pathway from the receptor cells of the inner ear to the auditory cortex has many neurons that are “running the wrong way.” That is, they go downward to the receptors rather than upward to the cortex. At first that seems hard to understand, but it is a key to the brain.

Reentry is a fundamental property of the human brain (Edelman, 1989). It is the reason why the classical EEG recorded from the scalp shows constant voltage oscillations. Scalp voltages come from tiny circuits of neurons in the cortex and its input hub: the thalamus. The cortex tends to send long branches to the thalamus, and the thalamus sends them back to the cortex. Those *reentrant* circuits generate voltage oscillations, as we will see later. All the standard EEG waves, like alpha, theta, and gamma, involve such reentrant oscillations.

We normally tend to think in terms of a one-way flow of signal traffic going from point A to point B, and it takes a little rethinking to understand that most brain pathways are two-way

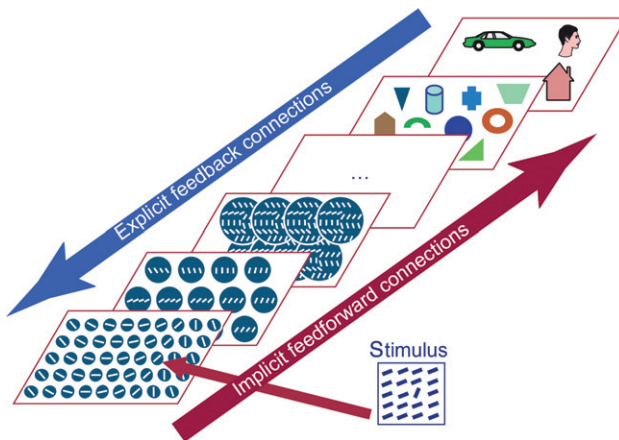


FIGURE 3.18 Two-way traffic between visuotopical maps. It's rare to find brain “traffic” that is not two-way. It makes sense to think of visual arrays, for example, as layers in a two-way network rather than a one-way path.

streets. The results are very interesting because neurons that are linked in both directions naturally set up *resonances* or *oscillations*.

As we will see later in this chapter, a natural “code” for the brain involves *linked arrays and oscillations*. When you record your voice and turn up the loudspeaker at the same time, you may get audio feedback, where the signal goes around and around until it gets very loud. That is essentially what linked arrays do with oscillations, except that biology learned a long time ago to make sure that feedback would not run out of control.

Two-way signal traffic means that much of the central nervous system should be viewed not as simple traffic arteries, but as reentrant loops—equivalent to neural networks with two or more layers (see [Figure 3.11](#)). From this point of view the brain is a vast collection of mutually echoing maps and arrays.

3.3 Top-down (expectation-driven) processing

The brain generates expectations about the world. Walking downstairs in the dark, we have expectations about every step we take. In dealing with ambiguities like the figures shown here, we constantly make predictions about which of two perceptual interpretations is the best one. Most words in English are ambiguous, so even as you are reading this sentence, you are resolving ambiguities. The brain is driven by more than just input; it has many ways of biasing choice-points by means of predictions and expectations. Lateral processing is also important, as we have seen, to sharpen differences between neighboring stimuli in the visual array. As we will see later, selective attention allows us to dynamically adjust our sensory biases (see [Chapter 8](#)), and long-term memory strengthens synapses that are associated with accurate perception.

Hierarchies are not rigid, one-way pathways. They allow signals to flow upward, downward, and laterally. A major function of downward flow of information in the sensory systems is the need to resolve ambiguities in the input. Ambiguities are common in visual scenes but also in language and the other senses. In motor systems, upward (bottom-up) flow of information is similarly useful to help make choices in output plans and motor commands.

Fuster (2004) suggests that both front and back of the cortex can be viewed as massive hierarchies of local hierarchies, starting from sensory receptors, and becoming more and more general as information flows upward in the sensory hierarchy ([Figure 3.19](#)). The motor hierarchy can be viewed as going in the opposite direction, ending up at motor neurons. However, as [Figure 3.19](#) indicates, information is exchanged between the two hierarchies in an ongoing perception-action cycle, from a low level (as in listening to one’s own voice speaking) to a very high level of planning, thinking, and anticipating the future.

4.0 NEURAL COMPUTING

Artificial neural networks have many practical applications, from face recognition to predicting the stock market. That is also scientifically important, because it shows that we understand enough about networks to see how the brain might do those things.

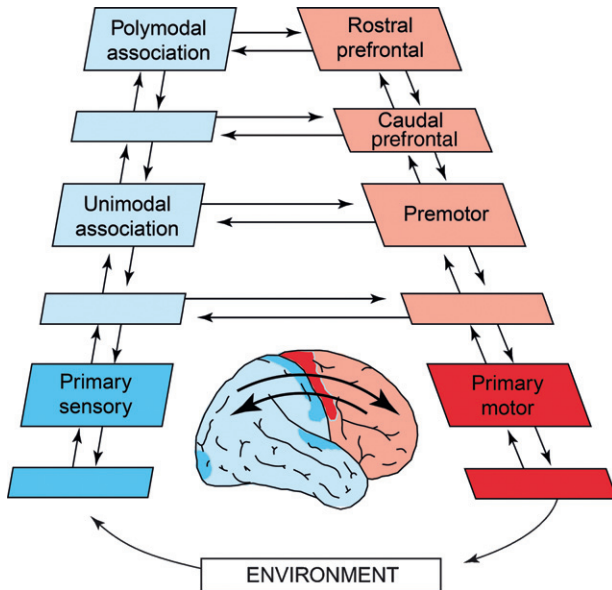


FIGURE 3.19 Sensory and motor hierarchies. Fuster (2004) suggests that all of the cortex can be thought about in terms of sensory and motor hierarchies, with information flowing between the posterior sensory regions and the frontal motor and planning regions. Source: Fuster, 2004.

After a slow start, the study of “neural nets” took off in the 1980s (Rumelhart & McClelland, 1986a, b). Connectionism has been the theoretical framework for much of this movement. Much of this chapter reflects lessons learned from the connectionist movement (see also Neural Darwinism, following). While neural nets were first explored in the 1950s, the early efforts encountered difficulties. By the 1980s, it became clear that adding an additional (hidden) layer would solve many of those problems and that feedback also helped.

Cognitive neuroscientists commonly focus on *biologically plausible* models: those that are based on the known properties of a specific set of neurons and their connections. However, artificial neural nets provide useful approximations to the reality. Figure 3.20 shows an example of a simple artificial neural net.

4.1 Some computational functions

The most obvious role of the neuron is signal transmission. However, our sensory receptors also convert light or sound (for example) into neuronal impulses. Neurons can control muscle fibers and hormone secretion. Thus neuron-like cells can be *signal transducers*, converting one kind of physical energy into another.

Neurons can also be thought of as computational switches, like the transistors that run a computer. Switches have ON and OFF states, and the firing of a spike is one possible switch. Whether the neuron sends a chemical signal to the next neuron may also act as a switch for the next neuron. These are only two out of many possible switching functions.

In the visual system, neurons line up in two-dimensional maps that represent the visual input. Early in the visual cortex the “visuotopical” maps correspond well to the retina in being very precisely “pixellated,” like an image on a computer screen. A single cell in V1 corresponds to a single cell in the retina. A very small visual stimulus, like a single star on a dark night, could trigger a pulse from a single receptor in the retina.

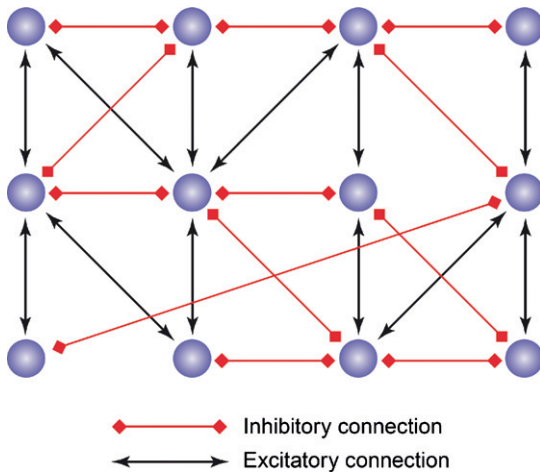


FIGURE 3.20 Artificial neural nets. A simple network. Note the combination of excitatory and inhibitory connections. Source: Palmer-Brown et al., 2002.

There are about a million light receptors in the fovea, the densest patch of the retina. We can imagine it as a $1,000 \times 1,000$ array of light receptors, where we can number each receptor by its position in a two-dimensional square with its origin (0, 0) at the center.

If a receptor at point (+100, +100) is triggered by the star, the corresponding point in V1 is also triggered. (V1 is the first visual map in cortex.) This is called “point-to-point mapping” or “labeled line coding.” At higher levels, visual maps respond to complex features like color, motion, and objects like coffee cups. Neurons can therefore encode spatial locations, the time of an event, and even higher-level features like color.

Synapses also have informational functions. The strength of a synapse is believed to store memory traces. For instance, the conditioned eye blink reflex is believed to strengthen synapses in the cerebellum. Episodic memories (memories of conscious experiences) are believed to be temporarily stored in neural activities in the hippocampus and very widely in the neo-cortex. Those learned activities are “consolidated” (solidified into permanent changes) during slow-wave sleep.

A recent insight is that neurons are also *oscillators*, a very important function in the brain. Individual neurons oscillate electrically when a spike travels down its axon. Groups of neurons, like the cortical columns we discuss later, can send out complex waveforms like the ones we can see in the EEG. Oscillatory signaling can spread from one array of cells to another, apparently in a very specific way. The cortex and its adjacent regions can be considered to be a giant oscillatory echo chamber, in which individual neurons and groups of neurons send and resend signals. Thus neurons and synapses perform many computational functions.

5.0 THE BRAIN CODE: MAPS + WAVES

Neurons can be coordinated in a number of ways. One is for large-scale rhythms to drive populations of neurons, like the conductor of a symphony orchestra. When many neurons fire in unison, their activity adds up, just as a large crowd of people sounds louder when they are chanting in unison.

There is a limit, however, to the way billions of neurons can be coordinated. Epileptic seizures have long been believed to be caused by neural scar tissue, called the epileptic focus, which sends out intense, slow, and regular waves that recruit more and more brain regions so that spreading populations of neurons begin to chant the same song. The result is a loss of consciousness and physical seizure activity.

Somehow the brain must coordinate thousands of neurons that work together to achieve a specific cognitive task, like perceiving a coffee cup. But the coffee cup ensemble cannot grow so large as to recruit all of the brain. It must be able to recruit new neurons and also leave those that are irrelevant to seeing a coffee cup.

In 1929, Hans Berger, a psychiatrist, first observed brain waves over the occipital cortex in his young son. Berger was able to do that because his equipment could amplify the small voltages involved. He was also lucky in that he was able to observe alpha waves, regular sine waves that oscillate between 8 and 12 Hz, when his son closed his eyes. When he opened his eyes, the alpha wave (arbitrarily named “alpha” because it was the first regular waveform found in humans) was interrupted by complex and fast activity, which were called beta and gamma waves.

For many years only “raw” EEG waves could be observed. Most raw EEG waveforms are complex, and regular waves like alpha live in an ocean of complex waves with many different origins, at many frequencies and amplitudes. The simple signals are swamped. However, when high-speed computers came into use, it became possible to analyze complex waveforms very quickly. What were originally simple-looking waves in EEG are now filtered from the complex waves of the full-spectrum EEG all over the head. We therefore tend to talk about “frequency bands” rather than simple frequencies to include anything between 8 and 12 Hz in the alpha band, for example. It is important to remember that our current way of slicing up the EEG frequency range is still somewhat arbitrary. There is no particular reason why alpha waves are called alpha waves. It is possible that we will learn to group the frequencies differently.

Table 3.1 gives a useful set of brain waves as we currently understand them. Regular EEG rhythms are now believed to signal distinct, coordinated processes. For example, a high density of gamma rhythms has been related to conscious visual perception and to the process of discovering a solution to a simple word problem.

Obviously, the brain must balance the degree of coordination against the need for local neurons to work on local functions. There must be a balance between neuronal integration and differentiation (Edelman & Tononi, 2000).

5.1 Synchrony and phase-locking

Regular EEG rhythms are now believed to coordinate widely separated cells and “cell assemblies.” For example, gamma rhythm has been related to conscious visual perception and to the process of discovering a solution to a simple word problem. Alpha rhythms are traditionally associated with relaxation, but they now seem to play many different roles. Theta rhythms coordinate the hippocampal region and the frontal cortex during the retrieval and consolidation of memories. The delta rhythm of deep sleep is believed to coordinate faster rhythms to facilitate consolidation of learned events (Kemp et al., 2004).

TABLE 3.1 EEG Frequencies and their Associated Functions

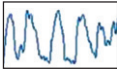
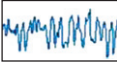
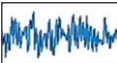
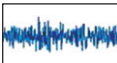
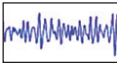
Name and example	Description
<div>Delta</div> 	<p>Delta is the slow wave characteristic of deep, unconscious sleep. It is less than 4 Hz, and similar EEG frequencies appear in epileptic seizures and loss of consciousness, as well as some comatose states. It is therefore thought to reflect the brain of an unconscious person.</p> <p>The Delta frequency tends to have the highest amplitude and the slowest frequency. Delta waves increase with decreasing awareness of the physical world.</p>
<div>Theta</div> 	<p>Theta activity has a frequency of 3.5 to 7.5 Hz.</p> <p>Theta waves are thought to involve many neurons firing synchronously. Theta rhythms are observed during some sleep states, and in states of quiet focus, for example meditation. They are also manifested during some short term memory tasks, and during memory retrieval.</p> <p>Theta waves seem to communicate between the hippocampus and neocortex in memory encoding and retrieval.</p>
<div>Alpha</div> 	<p>Alpha waves range between 7.5 and 13 Hz and arise from synchronous (in phase) electrical activity of large groups of neurons. They are also called Berger's waves in memory of the founder of EEG.</p> <p>Alpha waves are predominantly found in scalp recordings over the occipital lobe during periods of relaxation, with eyes closed but still awake. Conversely alpha waves are attenuated with open eyes as well as by drowsiness and sleep.</p>
<div>Beta</div> 	<p>Beta activity is 'fast' irregular activity, at low voltage (12–25 Hz).</p> <p>Beta waves are associated with normal waking consciousness, often active, busy, or anxious thinking and active concentration.</p> <p>Beta is usually seen on both sides of the brain in symmetrical distribution and is most evident frontally. It may be absent or reduced in areas of cortical damage.</p>
<div>Gamma</div> 	<p>Gamma generally ranges between 26 and 70 Hz, centered around 40 Hz.</p> <p>Gamma waves are thought to signal active exchange of information between cortical and other regions. It is seen during the conscious state and in REM dreams (Rapid Eye Movement). Note that gamma and beta activity may overlap in their typical frequency ranges, because there is still disagreement on the exact boundaries between these frequency bands.</p>

Figure 3.21 shows a simple hypothesis about how regular brain rhythms may coordinate the firing of millions of separate cells. Neurons that fire at the peak of the delta wave (for example) add a tiny amount of electrochemical activity to the whole chorus. Neurons that fire during the trough subtract their activity from the whole. Thus, neurons that fire in sync with the dominant rhythm are strengthened by feedback from millions of others that are following the same overall rhythm, while those that are out of sync are weakened. Such a mechanism would tend to reinforce a dominant rhythm.

But synchronized firing is not enough. Different coalitions of neurons must be able to represent inputs, which compete against other coalitions to recruit new members. Such a model is shown in Figure 3.22, where it supports a kind of Darwinian competition between different populations of nerve cells.

The brain is often called a massively parallel organ, because there is no central command post that tells all the neurons what to do. There are, however, a number of ways in which

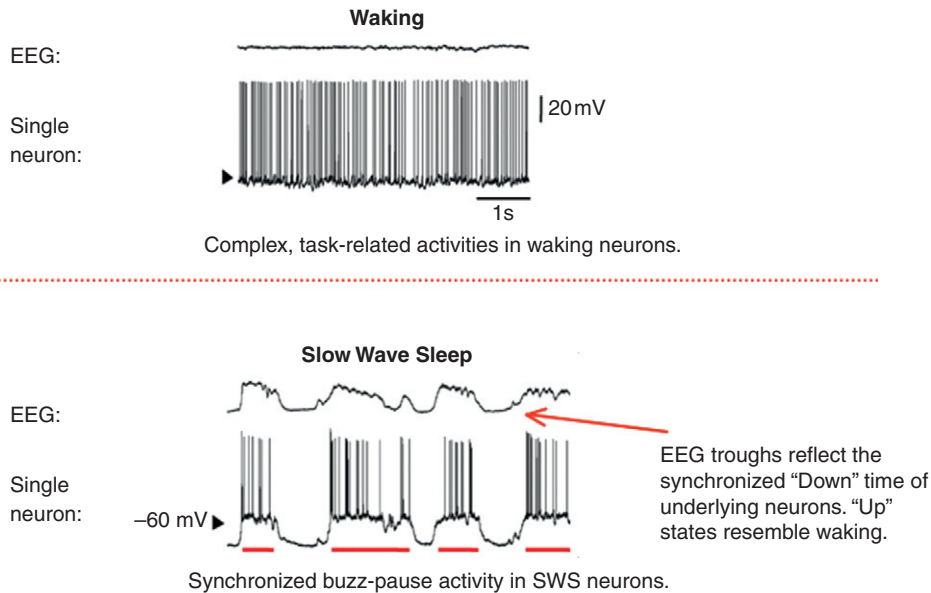


FIGURE 3.21 EEG and single-unit activity in waking and deep sleep. Conventional EEG measures the brain's electrical field over the scalp. Each EEG trace in the figure is a complex sum of underlying neuronal activity in the upper layer of cortex. Slow-wave sleep EEG reflects the simultaneous 'buzz' and 'pause' of billions of neurons, also called 'up' and 'down' states. Because waking-state neurons do not fire and pause synchronously, their voltages do not add up to large waves. The waking EEG looks small, irregular, and faster than slow-wave sleep. It is believed that waking (and REM dreaming) therefore involves more differentiated information processing in much the same way that a stadium full of talking people serves to process more information than the same people all chanting in unison. The unison chanting is largely redundant (you can predict the crowd chants from just one person) so the information content is lower (see Section 6.2). Source: *Adapted from Steriade, 2006.*

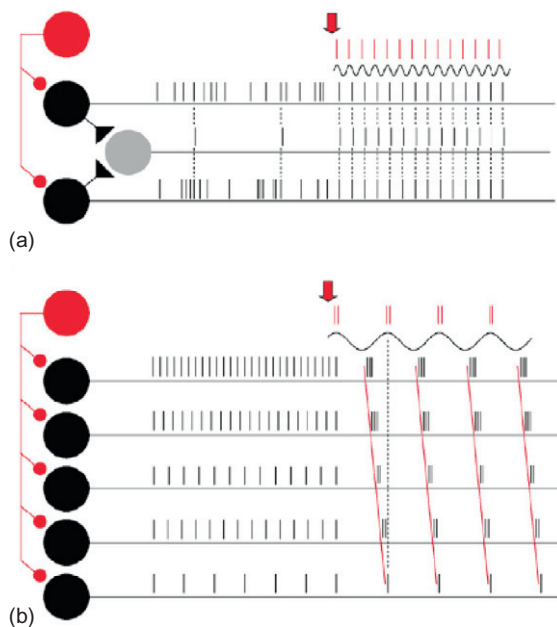


FIGURE 3.22 Inhibitory cells synchronize excitatory neurons. How inhibitory neurons drive synchrony in excitatory cells. (a) Coding by synchrony. If two excitatory cells (black) display random spike trains, they will rarely drive a common downstream cell above threshold (gray). By contrast, when synchronized by an inhibitory interneuron (red) these neurons, firing at the same overall rate, will now reliably activate the downstream neuron. (b) Phase coding. If five pyramidal neurons (black) are firing at different rates, the introduction of a rhythmic inhibitory cell will tend to drive the excitatory cells to fire at the same time. Source: *Mann and Paulson, 2007.*

neurons can be coordinated. As we mentioned earlier in the chapter, one way is for large-scale rhythms to pace populations of neurons, much like the conductor of a symphony orchestra. When many neurons fire in unison, their activity adds up, just as a large crowd of people sounds louder when they are chanting in unison. There is a limit to this, however. Epileptic seizures have long been believed to be caused by neural scar tissue, called the epileptic focus, which sends out intense, slow, and regular waves that recruit other brain regions, so that spreading populations of neurons begin to chant the same song. The result is a loss of consciousness and physical seizure activity.

Obviously, the brain must balance the degree of pacing and coordination against the need for local neurons to work on local functions. There must be a balance between *integration* and *differentiation* (Edelman & Tononi, 2000).

6.0 LEARNING AND ADAPTATION

A striking feature of animal behavior is flexibility—to learn which cues will bring pleasure, which will bring pain, and which are unreliable predictors of either. Added to this, environmental cues can vary across days and seasons, and social relations keep changing across the lifetime. An action that was previously a reliable source of reward may become barren. Animals must be able to learn that. A key feature of the brain is its adaptability.

The brain learns by changing the efficiency of millions of synapses. The basic idea of “synaptic efficiency” is that signals flow faster from one nerve cell to the next one. There are many ways to make that happen. One is to grow more synapses between neurons. Another way is to supply more glutamate to cells in a circuit.

6.1 Hebbian learning: “Neurons that fire together, wire together”

It is plausible that neuronal activity patterns are learned when they are used more often than others. Donald Hebb proposed in 1949 that assemblies of spiking cells could learn an input pattern by strengthening the connections between cells that fire at the same time. This idea is encoded in the slogan that “neurons that fire together, wire together.” It is a useful learning method for neural networks, and there is now direct evidence for Hebbian learning in the nervous system.

The key idea in Hebbian learning is that synaptic connections are the physical substrate of learning and memory. The transient connections are thought to be mainly electrochemical, while more lasting ones are thought to require protein synthesis. Long-term increases in excitation from one neuron to another are called *long-term potentiation* (LTP). Long-term decreases are called *long-term depression* (LTD). There is evidence for both.

Learning has been studied intensively in layered arrays of simulated neurons. When neurons trigger other neurons, the resulting activity may be stable or unstable. Unstable patterns tend to die out, while stable patterns remain for some period of time. Such stable patterns are called *cell assemblies*. Hebbian cell assemblies may involve neighboring cells, or they may

involve cells that are far from each other. Cell assemblies that combine *both* excitatory and inhibitory connections tend to be more stable and lasting.

Figure 3.23 shows findings that seems to confirm the model, with actual strengthening of connection probabilities (“weights”) in the hippocampus of a rat. In the three dotted circles of Figure 3.23 each dot represents 42 neurons that consistently responded to a specific place in the rat maze when the rat entered the maze.

The dotted circle corresponds to correlated firing rates between the dots (the place neurons) for one place in the maze. The thickness of the line between two points corresponds to the correlation between two sets of place cells. Notice the similarity between RUN (the practice period) and POST (a period of slow-wave sleep that is believed to involve a replaying of the learned information).

The most important point in Figure 3.23 is the similarity of the thicker lines between RUN and POST. They show more correlated firing between place cells that were activated together during the learning period: “Neurons that fire together, wire together.”

6.2 Neural Darwinism: survival of cells, synapses, and even dynamic activity

The neuroscientist Gerald Edelman has proposed that the brain is a massive *selectionist* organ. Edelman’s theory is called *Neural Darwinism*, since it suggests that neurons develop and make connections following Darwinian principles. In evolution species adapt by *reproduction*, followed by *mutations* leading to diverse forms, and finally *selection* among the resulting repertoire of slightly different organisms. Over long stretches of time, this growth-and-weeding process yields species that are well adapted to their niches.

A similar process occurs in the immune system, where millions of immune cells adapt to invading toxins. Cells that can successfully match the invaders multiply, while unsuccessful ones dwindle in number. The immune system can therefore learn to recognize and combat novel invaders. *Selectionism* leads to flexible adaptation.

According to Edelman (1989), the brain has two stages of selectionist adaptation. The first begins long before birth, when the first neurons are born, multiply, differentiate, and are selected if they fit their local niches. The outcome of this stage is a vast set of neurons that look like a brain. The second, overlapping stage, begins when neuronal connections are

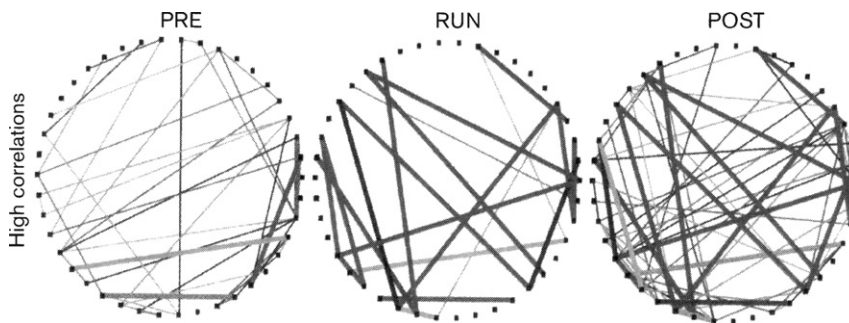


FIGURE 3.23 Observed Hebbian learning. Strengthening of neuronal connections has been observed directly in hippocampal neurons in a rat. Source: Sutherland & McNaughton, 2000.

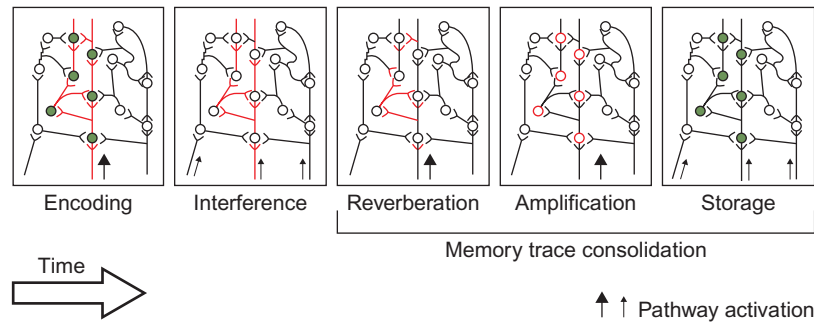


FIGURE 3.24 Neural Darwinism in learning: stages of encoding a neural activation pattern until dynamic synaptic activity allows permanent connections to be strengthened. Source: *Ribeiro et al., 2004*.

made: synapses. Adaptive connections tend to survive, while others die out. Darwinian selection therefore operates both developmentally and as a result of learning (Figure 3.24).

Two-way connections between neuronal maps allow for reentrant (two-directional) processing. If a reentrant process is stable, it will tend to survive among all the other transitory waves of activation in the brain. If not, it will fade away.

These ideas have been refined by brain studies and computer simulations. A series of robots have used selectionist principles to simulate how brain regions seem to learn.

7.0 SUMMARY

How can nerve cells perform cognitive functions, like perception, memory, and action? That problem has not been solved in all its richness. However, we have made progress.

Arrays of neurons support spatial coding of information, but there is temporal coding as well. The rhythms of EEG are believed to correspond to massive coordinated activities in populations of neurons. Recent research suggests that gamma activity may be involved in sensory integration and theta has been associated with retrieval from long-term memory.

8.0 STUDY QUESTIONS AND DRAWING EXERCISES

8.1 Study questions

1. Describe an integrate-and-fire neuron.
2. What is lateral inhibition and how does it relate to perception?
3. Explain how sensory and motor regions can be viewed as hierarchies.
4. Describe the role that reentrant (two-way) connections play in brain function.
5. What is Neural Darwinism and how does it work?
6. List three features of sensory systems.
7. What slogan describes Hebbian learning?

8.2 Drawing exercise

Label the parts in [Figure 3.25](#). You may want to draw the neuron itself as well, to get a better sense of the typical shape of a pyramidal neuron, the “workhorse neuron” of the cortex.

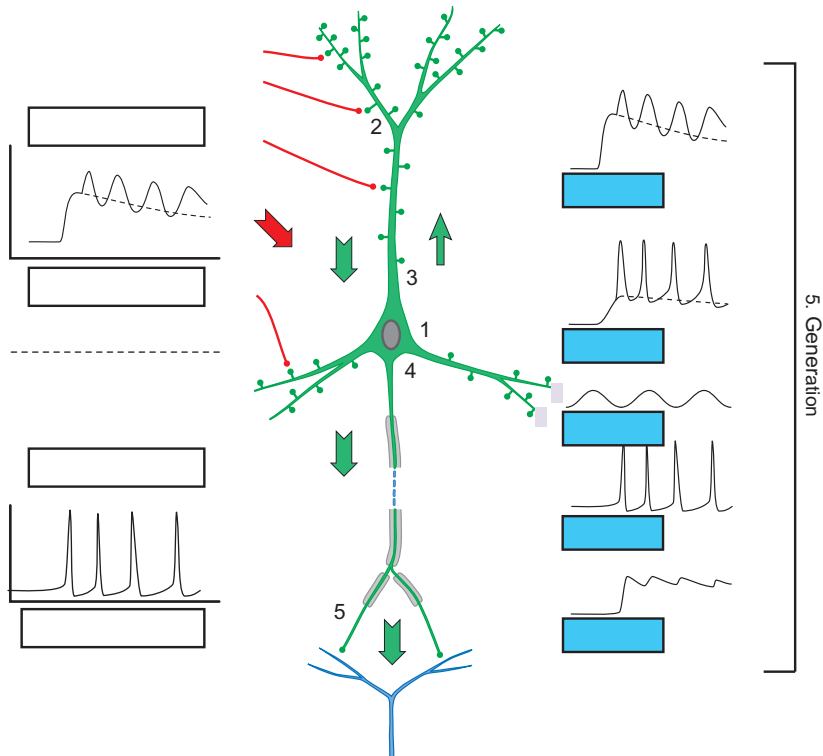


FIGURE 3.25 Label the parts of the figure.

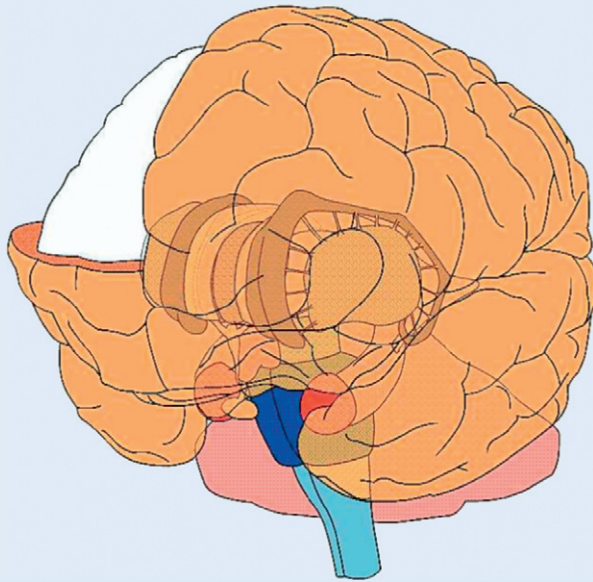
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The brain

O U T L I N E

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THE BRAIN



Looking through the gray outer layer of the cortex (beige color), you can see a mass of white matter that consists of billions of axons from the cortical cell bodies. The long axons are covered with white protective cells, which give the “white matter” its color. The surface “gray” layer is only a few millimeters thick. Can you identify the internal structures of the brain? We will try again at the end of this chapter.

Source: left: Baars & Fu, 2011, with permission; right: Google 3D Warehouse, Copyright-Free Archive

1.0 INTRODUCTION

We’ve seen how neurons weave together to perform a host of functions. The human brain emerged after millions of years of evolutionary experiments with neurons, including neurons as stimulus receptors, neurons as muscle controllers (motoneurons), neuron arrays and hierarchies, pathways, and more. Humans have many features of our ancestral brains, including brainstem centers for basic survival functions like breathing, heart rate, and more.

On top of the brainstem, newer structures mushroomed up and out, including the “paleo-cortex” (ancient cortex), which includes the hippocampus and amygdala. We have seen the history of two patients, Clive Wearing and HM, who suffered from damage to those regions, leading to an inability to remember their everyday experiences. The even larger, outwardly

visible cortex grows from the earlier paleocortex. This “neocortex” (new cortex) is a six-layered sandwich, with many more neurons and synapses.

In humans, the frontal lobes expand even beyond the primate brain, making rapid cultural evolution possible. Our frontal lobes support the ability to speak through Broca’s area. Language is a major key to human culture, and is believed to arise only a few hundreds of thousands of years ago—compared to 200 million years for mammalian evolution. Evolution takes thousands and millions of years, while cultural changes can happen over years and decades.

In this chapter we look at the structure of the brain, which packs billions of neurons into a small space above the nasal cavities. The brain is suspended in a watery medium, richly fueled with oxygen and glucose, and cradled in a protective vessel made of bone, muscle, tough connective tissues, tendons, and the like. Inside the cranium, billions of neurons are supported by even larger numbers of glial cells that wrap around the long and delicate axons.

We encourage you to use all kinds of memory and visualization aids to clarify for yourself how complex organic shapes fit together. For example, you can hold up your fists to remind yourself about the orientation of the two hemispheres. We also encourage you to make your own rough sketches as we go along. The rough shapes are more important than the small details.

As you can see from the figure at the beginning of the chapter, the visible part of the outer brain covers several levels of deeper structures. Later in this chapter we will see how the brain looks when we take off each evolutionary layer, until we see the brainstem itself.

In [Figure 4.1](#), notice that the brain is the largest outgrowth of the nervous system. In fact, the whole body is pervaded with neurons and their tiny branches. Neurons make up a vast communication system throughout the body.

Remember that “nerves” are large *bundles* of axons that grow from single neuronal cell bodies. “Nerves” are not single cells but might combine a million axons in a single bundle. As you can see in [Figure 4.1](#), right panel, the cranial nerves—vision, hearing, smell, taste, and tactile signals from the head region—all enter the brain through tiny openings in the cranium. (Also see the perspective shown in [Figure 4.5](#).)

The cranial nerves enter the brain at the bottom because the brain evolved upward, while the sensory channels kept the same relative position. In addition, the body senses from the torso, arms, and legs enter the brain in the same general area through the spinal cord. Both the cranial and the spinal nerves are therefore visible at the bottom of the brain, as if some biological engineer neatly tied together all the wires coming into your personal computer.

The same thing is true on the output side, where nerves control our muscles. The major cranial motor nerves all emerge from the bottom of the forebrain, the giant mushroom we usually just call “the brain.” That means that your tongue movements, for example, are also controlled by cranial nerves. Your vocal tract, the most complex and highly coordinated motor system human beings have, is also controlled by cranial nerves. When a dentist injects a local anesthetic in a very specific location in your mouth, a branch of a sensory cranial nerve is temporarily blocked.

The classical five senses are only a convenient simplification. Each of the classical senses has its own subsenses, some of which have only been discovered recently. For example, there are light-sensitive cells in your retina that are not for ordinary vision but which tell your circadian rhythm system when it’s time to go to sleep.

The tactile senses include touch, exploratory (haptic) shape sensing, pain perception, and even tickle perception. The pain system is itself a complex and medically very important network that pervades the human body.

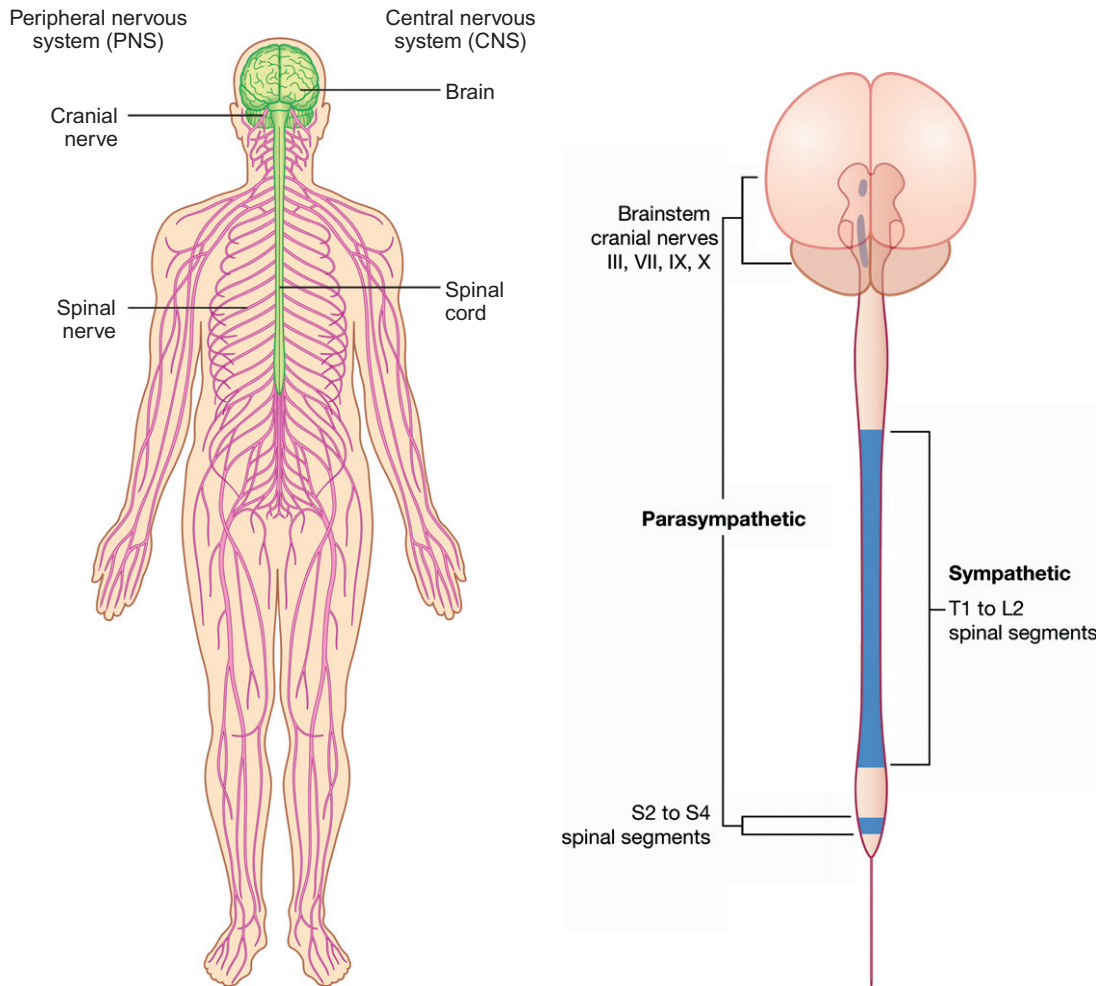


FIGURE 4.1 The central and peripheral nervous systems. The nervous system pervades the human body. Left: Its two main parts are the central nervous system (CNS), the brain and spinal cord, and the peripheral nervous system (PNS), which contains the autonomic and peripheral sensory and motor system. Right: The central nervous system includes the spinal cord and the brain. Source: *Standring, 2005*.

There is only one cranial nerve that goes directly into the body, called the vagus nerve. (*Vagus* means “wanderer,” as in the word *vagrant*.) The vagus nerve is important for *interoception*, the perception of the inner feelings of the body. Interoception is quite different from *exteroception* (vision, hearing, and all the others). It may be closely tied to the emotions.

The autonomic nervous system (ANS) is an independent (autonomous) division of the peripheral nervous system that helps to accelerate and decelerate body functions. If you need to run, fight, or mobilize your body for rapid actions, the autonomic nervous system gets involved, using the hormone adrenaline (epinephrine). If you need to decelerate, to recharge

your batteries and take it easy, another part of the ANS gets involved. You can see this in [Figure 4.1](#), right panel, in the sympathetic (arousing) and parasympathetic (relaxing) nervous systems. As you can see, the nervous system is very clearly organized.

2.0 THE CORTEX

The cortex is the outer “skin” of a brain that has evolved over hundreds of millions of years. While the six cellular layers of the cortex are only a few millimeters deep, they send out a vast number of microthin fibers to the thalamus and other brain “hubs.” It is those tiny nerve fibers that are surrounded by white support cells, giving the impression that most of the brain is filled with white tissue.

The fetal brain grows from a very small neural “crest” to billions of neurons, much like an ancient city, with later levels of buildings and streets covering an older core. It is useful to start with a standard view of the two hemispheres, as in [Figure 4.3](#).

Can you identify the major landmarks? If you have trouble visualizing the spatial orientation of the two brain figures in [Figure 4.2](#), it’s convenient to use your own hands or fists. Remember that each hemisphere has ballooned outward, so both the outside surface and the medial (midline) surface of each hemisphere consist of a thin cortical skin.

In exploring a new city you may want to pay special attention to prominent landmarks that are so distinctive that you cannot confuse them. [Figure 4.2](#) shows major landmarks that are

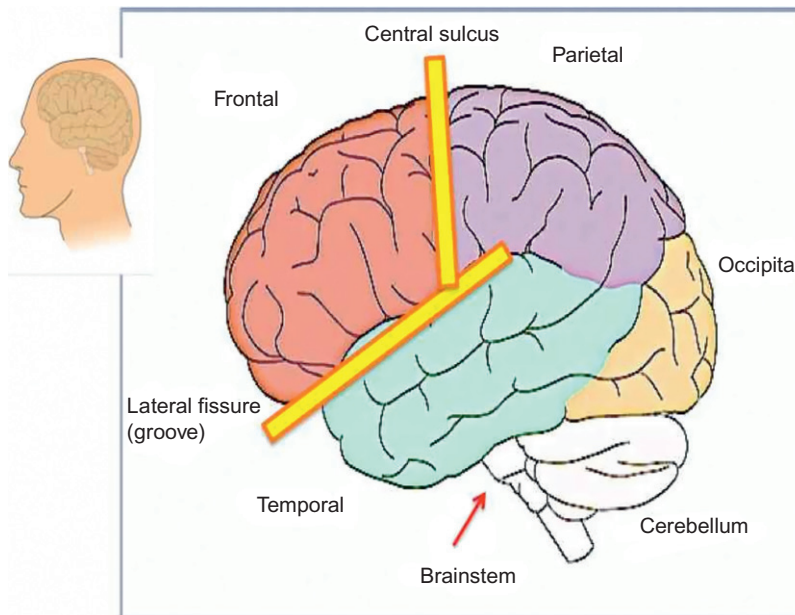


FIGURE 4.2 Major landmarks: lobes and fissures (grooves). Here we show a view of the left hemisphere with the four major lobes, the biggest divisions of the cortex. However, there are hidden regions as well, including the hippocampus, amygdala, and insula. Notice that the inset head is facing left. Source: *Baars and Fu, with permission.*

widely used to stay oriented to the brain. Remember to make a rough sketch of the major landmarks that look the most important. As we go along, you can add details to your sketch.

We usually show the brain from the left side, where the language areas tend to be located. For medical purposes it's important to know if brain damage might affect speech output or input. Scientifically we may use the language regions to explore executive functions. People talk to themselves during all their waking hours, and self-directed talk is one way we plan our way through the world.

Many brain structures look doubled, like mirror images of each other. The two halves of the cortex are a good example of the doubled structure of most of the brain. As you can see from [Figure 4.3](#), the two hemispheres have somewhat different specializations. Some of those are

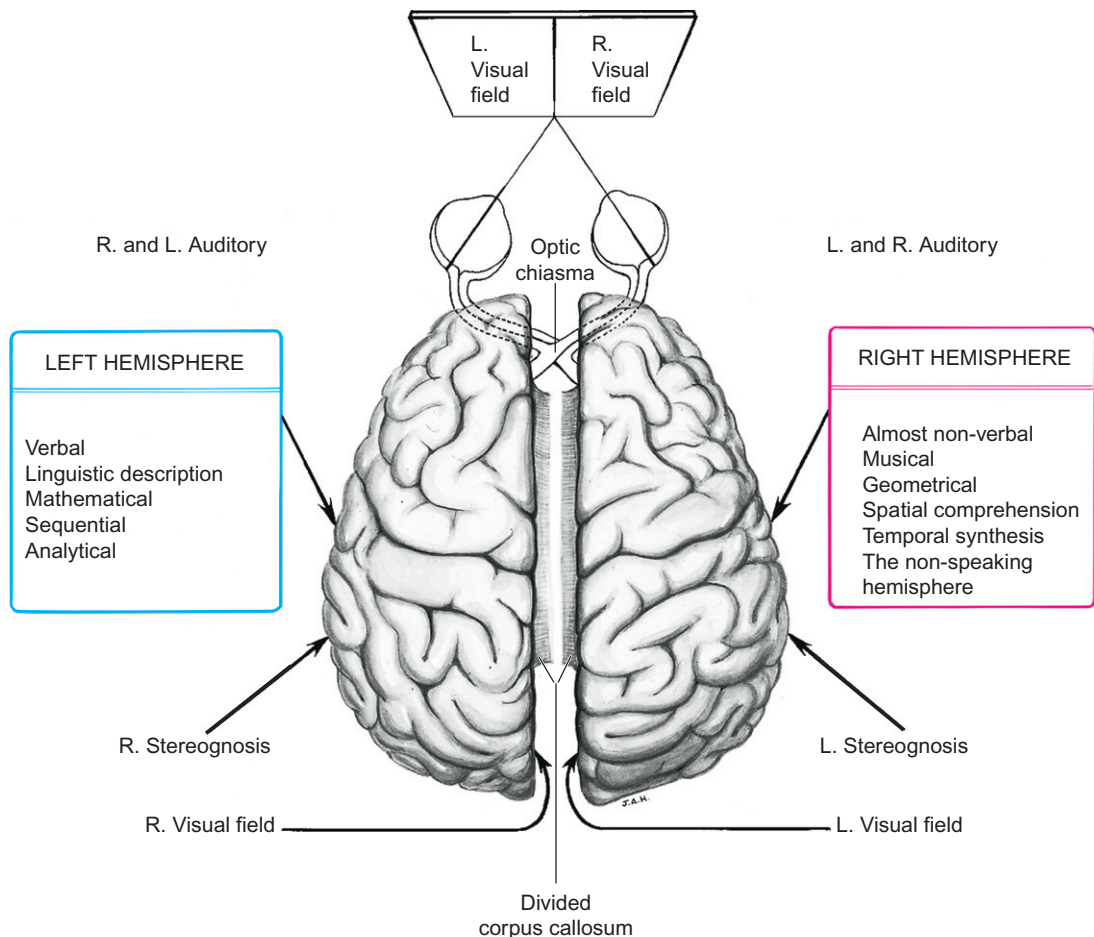


FIGURE 4.3 The two hemispheres and the bridge between them, seen from the top. A schematic drawing of the halves of the cerebral cortex, showing some major functions of the right and left hemispheres. Note the massive bridge of the corpus callosum connecting the two sides. The two eyes on top converge on a single object to enable stereoscopic depth perception. Source: *Standring, 2005*.

very clear—like the speech output function of the left hemisphere in most people. The sensory and motor systems cross over so the right hemisphere (RH) receives direct information from the left half of the visual field. The left hemisphere (LH) receives visual information from the right half of the visual field. Similarly, motor control of the hands and feet cross over. The right hemisphere controls the left hand, and vice versa.

The reason for these crossovers is not known. It is an evolutionary feature, and it is found even in some songbirds. Most other cortical functions are shared by the two hemispheres. For example, both hemispheres can perceive and understand language. But only one (usually the left side) controls speech output. This is a very important feature of the human brain.

2.1 The great bridge between the hemispheres

The hemispheres are separate, divided by the longitudinal valley that runs between the two hemispheres from the front to the back of the brain. What unifies these two halves is the great bridge between the hemispheres, the corpus callosum, or “calloused body” (see [Figure 4.3](#)). The great bridge has about 100 million fibers, with equal numbers beginning from RH going to the left and from LH flowing to the right.

These fibers connect the hemispheres in an orderly way, with regions in each cortical patch connecting similar patches on the opposite side. Thus the left occipital area connects directly to the right occipital area, and so on. The result is that the two hemispheres tend to dance in close synchrony with each other.

A useful analogy is a large city divided by a river. As long as traffic is flowing smoothly across the bridge, it is hard to tell if the financial center is on the left bank and manufacturing is on the right bank. As long as traffic is flowing well, the city works as a single, unified system. But if a section of the major bridge falls down in an earthquake, the city behaves like *two different* systems.

As long as the corpus callosum is intact, it is hard to tell which hemisphere is doing what because the two hemispheres are constantly talking to each other. We can see the two halves of the cortex disconnected when the corpus callosum is cut. The most famous examples involve “split brain” patients who have had surgery to cut the corpus callosum. Split brain surgery can help to control epileptic seizures, which are giant electrical storms that often start on one side and spread to the other.

Like the case of Phineas Gage (see [Chapter 1](#)), after split brain surgery, patients and doctors may not notice functional problems. Like the city across the river, the brain learns all kinds of spontaneous “workarounds” that can work so well that we may not even notice any difference—unless we look very carefully.

In the case of split brain surgery, patients may learn to move their eyes from side to side so that the bridge between the hemisphere is not even necessary to combine the two sides of visual space. Or they may place their hands across the midline so that one hemisphere can see the hand that is controlled by the other one. The speaking hemisphere may even talk out loud to the hearing hemisphere (often the left side talking to the right side). Since both sides tend to have speech input (perception and comprehension), that is one way in which split brain patients may achieve an integrated experience of the world.

Split brain patients reveal their divided functions when we carefully isolate their input and output channels. For example, if patients receive separate information from the right half

versus the left half of their visual fields, we can see two separate cortices working separately. Patients can report one side verbally (which side do you think?) and another side by moving one of their hands (which side?). If their hands are kept visually hidden under a table, it is easy to show that each half cortex controls the hand on the opposite side.

One important lesson from split brain patients is that the brain tries to make up for missing information. We have already seen that in the case of Phineas Gage, who seemed to be normal after his injury, though his personality went through a radical change. We've also seen the cases of Clive Wearing and HM, where loss of the hippocampal regions on both sides caused very severe deficits of episodic learning and recall. However, while Clive Wearing seems very upset about his deficit, HM seemed to show less concern. We do not know why. It is an important feature of brain damage that some people are aware of their impairments while others may never realize that anything is wrong.

The brain looks complicated, but there are some basic organizing principles. One is that because it grew upward both over evolutionary epochs and during fetal development, each successive story of the house built on the lower one. That is why the large highway system, both incoming and outgoing, must flow through the brainstem and nearby regions at the bottom of the brain.

In [Figure 4.4](#) you can also see the two symmetrical “striped” structures, looking like the halves of an ostrich egg, at the bottom of each hemisphere ([Figure 4.4](#)). What major brain structures are we looking at? Notice that the optic nerve running from the back of each eye splits in half. Then each inner (nasal) half will cross to the other side.

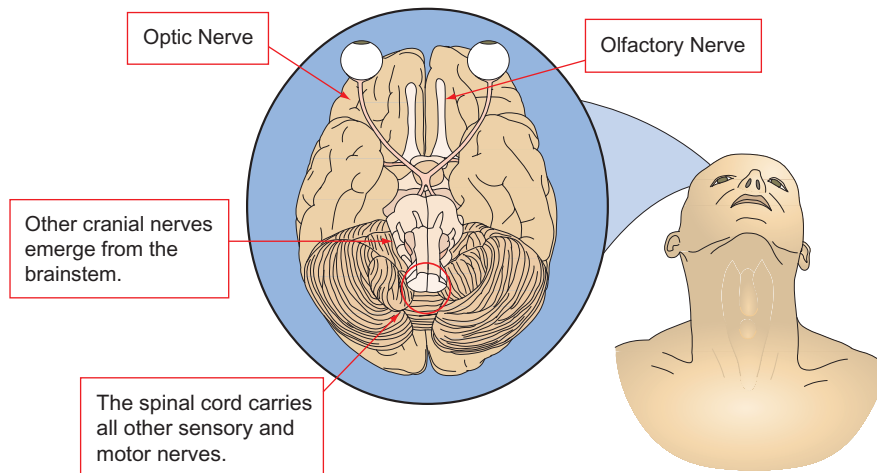


FIGURE 4.4 All sensory and motor nerves flow through the bottom of the brain. Note the cranial nerves and spinal nerves entering the bottom brain. The spinal cord flows directly into the brainstem (the widening trunk of the tree). The cranial nerves come from the eyes, inner ears, tongue, mouth and nasal cavity, face and head, and even the vocal tract. Compare this to [Figure 4.1](#), right side, which shows more of an overview. Source: Baars & Fu, 2010, with permission.

Notice that input and output channels freely cross over the midline, and come and go through parts of the brain that we are not subjectively aware of. Most people do not know that their sensory nerves run through the bottom of the brain, just behind the throat. But as long as the brain “knows” what connects to what, there’s no problem with wires and cables running one way or another. You could have a video camera pointing at your face and turn your computer upside down. As long as your computer kept track of which pixels belong where, this is not a problem.

While it is often useful to think about brain territories by geographical analogies, the brain, like the world, is a dynamic place. New streets are built and old ones are rebuilt. Houses and their residents appear and disappear. Until about a decade ago, it was believed that neurons did not change in the adult brain, but we now know of a number of ways in which neurons continue to grow, migrate, connect, disconnect, and die, even in the healthy mature brain. The brain is never frozen. These dynamic aspects of the brain can be seen even at the level of the cortex (Figure 4.6).

Remember that with the naked eye, the cortex looks like a double balloon (left and right hemispheres), but the skin of the balloon keeps an amazing consistency throughout. The mammalian “neocortex” is six layers deep. Layer I consists of horizontally spreading dendrites (input branches) that interweave so densely that they form a kind of cloth, a “felt-work” or *neuropil*. Layers IV and VI also have a great many horizontal connections. Notice at the bottom that long wires (axons) are coming and going to and from the thalamus, while others are going straight down to the brainstem and spinal cord. Finally, billions of fibers are going from cortex to cortex, linking the two hemispheres and also connecting the front and back.

The six horizontal layers of cortex are also organized vertically into columns, like barrel-shaped cylinders (see Chapter 3). These often contain closely related neurons, such as visual cells that respond to different orientations of a single line. Columns may be grouped into hypercolumns, which may be part of even larger clusters. Thus cortex is like a layer cake. It has both a horizontal organization into six layers and a vertical one into columns, hypercolumns, and entire specialized patches.

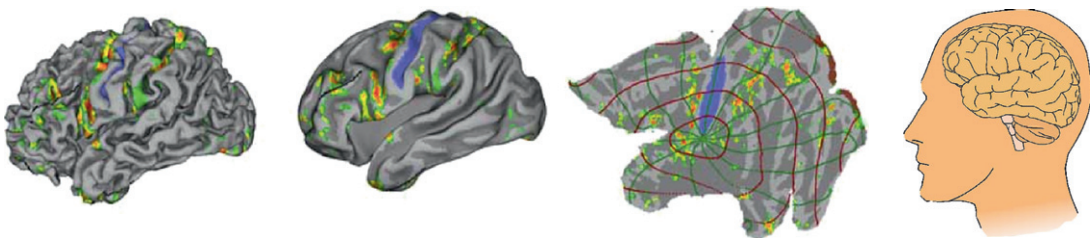


FIGURE 4.5 A mathematically flattened hemisphere. The cortex is actually a flat surface with six layers of cells. In most mammals, the cortex actually looks flat because its surface area fits inside the skull. But in humans, whales, and some other species, there is not enough room to spread the cortex out to its full extent. It is therefore folded in the way we normally see. However, it is still important to understand that its billions of neurons are lined up as a flat, six-layered sandwich of cells, with very long axons that take up most of the internal space. The cortex is a folded sheet of gray matter that measures roughly 2 feet by 2 feet, if unfolded. To fit into the human skull, the flat cortex is folded into hills (gyri) and valleys (sulci). Source: Van Essen laboratory, Washington University Saint Louis (<http://brainvis.wustl.edu>)

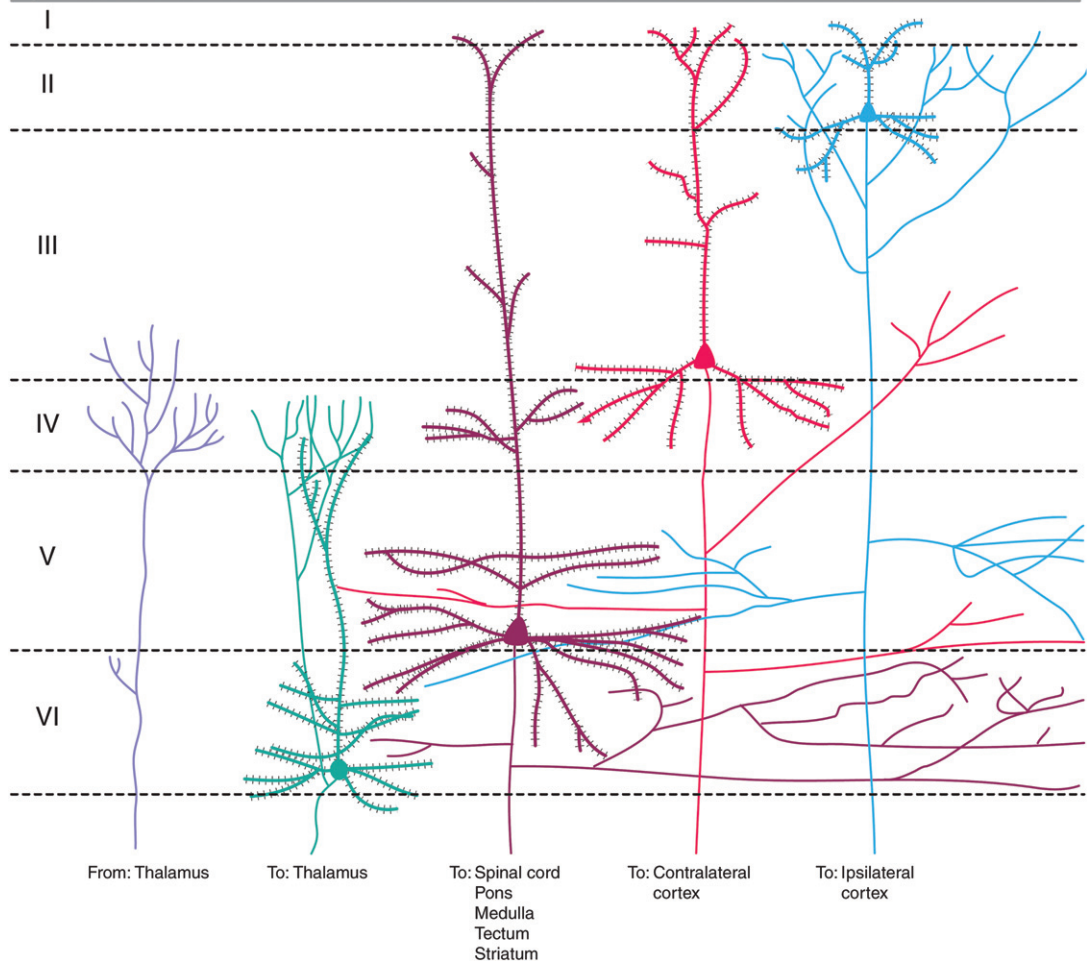
Cortical
layer

FIGURE 4.6 A schematic drawing of long-distance neurons in the cortex (pyramidal). These send their long axons to and from the great input hub, the thalamus, as well as to the brainstem and spinal cord, and to other regions of the cortex. That is why the cortex and thalamus are often considered to be a single, unified system. Note that the six layers are numbered in Roman numerals, with layer I at the surface and going down to layer VI. Source: *Standring, 2005*.

2.2 The cortex's maps

Figure 4.7 shows two famous body maps in the cortex. These were discovered by Wilder Penfield when he stimulated these cortical regions in waking patients preparing for epileptic surgery. In the sensory map, patients reported sensations in the body parts being stimulated

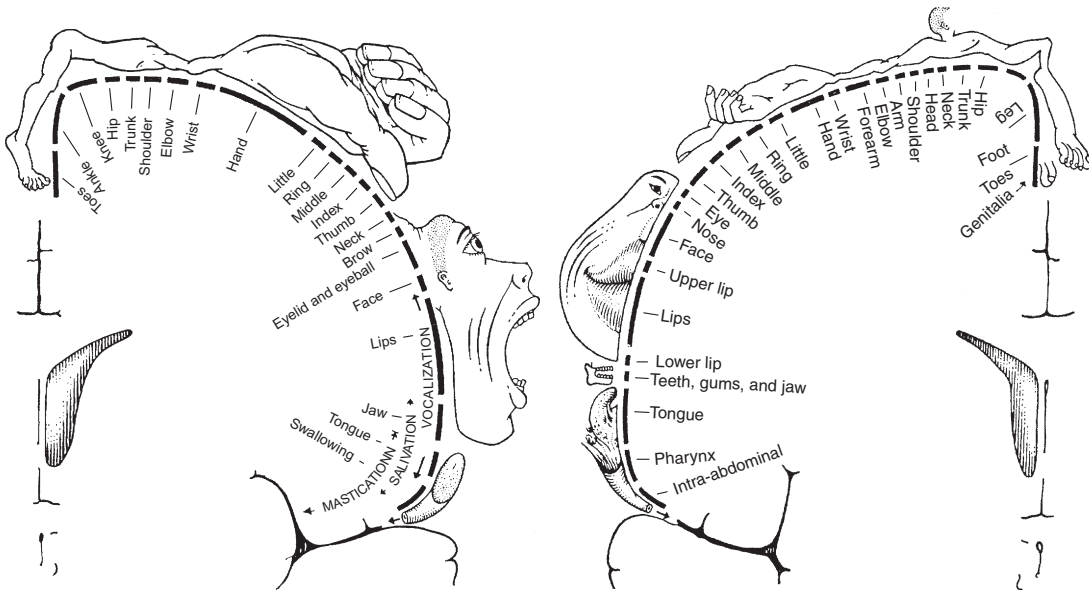


FIGURE 4.7 Two body maps: sensory and motor. The brain has many topographical maps, corresponding to the sensory input arrays for vision and touch, and the motor arrays for controlling our skeletal muscles. The body maps shown here are often called the “sensory and motor homunculus” and show the representation of body areas in the cortex. Note that some body areas, such as the face, have a disproportionately larger representation than other areas, such as the trunk. Source: *Standring, 2005*.

with a small electrical current. In the motor maps, their hands or feet might move, but patients often felt they were not in charge of the movements. The “homunculi” shown here directly correspond to the sensory input and muscle output of the cortex. When Penfield stimulated similar maps in related regions, patients might feel an urge to move their hands, for example, without actually having to move them.

These two *homunculi* (“little men” in Latin) are located immediately next to the central sulcus shown in [Figure 4.3](#). The central sulcus is a useful landmark. Cortex behind it is mostly sensory, and cortex in front of it is mostly motor or future-directed for planning and executive control.

The brain has many visual maps, generally coordinated with the visual input. It also has many body maps like the ones in [Figure 4.7](#). [Figure 4.8](#) shows the insula, a hidden “island” of cortex that is very important for interoception (feeling the inner body, as in feelings of nausea or satiety, and perhaps feelings of fear and love). The front half of the insula is especially important for sensing the “inner self.” The body maps of the insula are not as accurate as the homunculi shown in [Figure 4.7](#), but they are very important functions. They may take input from the vagus nerve, the only cranial nerve that goes down into the body, including the digestive tract, the diaphragm, stomach, and heart. Before you go on to take away the levels of the brain from top to bottom, you may want to review this section.



FIGURE 4.8 A dissected human brain, showing the insula (or “island”) after removing an outer slice of the frontal and temporal lobes. The insula has body maps, including interoceptive maps of the inner core of the body. Source: *Standring, 2005*.

3.0 BELOW THE CORTEX

We can follow the brain from top to bottom to show the structures that are normally hidden by the giant mushroom of the cortex. We encourage you to draw these levels of the giant tower of the *neuraxis*—the central bundle of billions of neurons that make up the spinal cord, the brainstem, the olfactory brain (hippocampus and amygdala), the diencephalon (thalamus), and the cortex ([Figure 4.9](#)). If you can draw these basic shapes, you will have a solid framework for cognitive neuroscience.

If you think of the brain as a towering building with seven or eight stories, you can understand its evolutionary and individual history. The idea of a tower suggests that lower regions like the brainstem are more ancient than higher regions, such as the frontal cortex. Basic survival functions like breathing are controlled by neural centers in the lower brainstem, while the large prefrontal cortex in humans is a later addition. The prefrontal cortex is the most recent part of the frontal lobe, immediately in front of the motor cortex (see [Figure 4.3](#)). Thus, as we know from the case of Phineas Gage (see [Chapter 1](#)), local damage to the prefrontal cortex has little impact on basic survival functions, but it can impair sophisticated abilities like decision making, self-control, and even personality.

Just as the brain contains many signaling highways, it also contains many hubs—places where multiple highways come together, and from which they spread out, like an airline hub or a television broadcasting station. As we will see, the thalamus is a major sensory hub.¹ But in [Figure 4.10](#), on the outside of the thalami, we see the basal ganglia, which are especially important as an output hub. The frontal lobes are concerned with planning and motor control, and they have a constant

¹ Notice that we refer to “the thalamus” as if there is only one. That is somewhat misleading. It’s important to remember that most brain structures are paired. There are also two thalami, two sets of basal ganglia, two hippocampi, and two amygdalae. In fact, even the parts of the brain that do not look doubled generally turn out to have two symmetrical halves upon microscopic examination. The brain is very much like Russian dolls that have increasingly smaller dolls inside them. For our purposes, however, we are interested only in the biggest dolls.

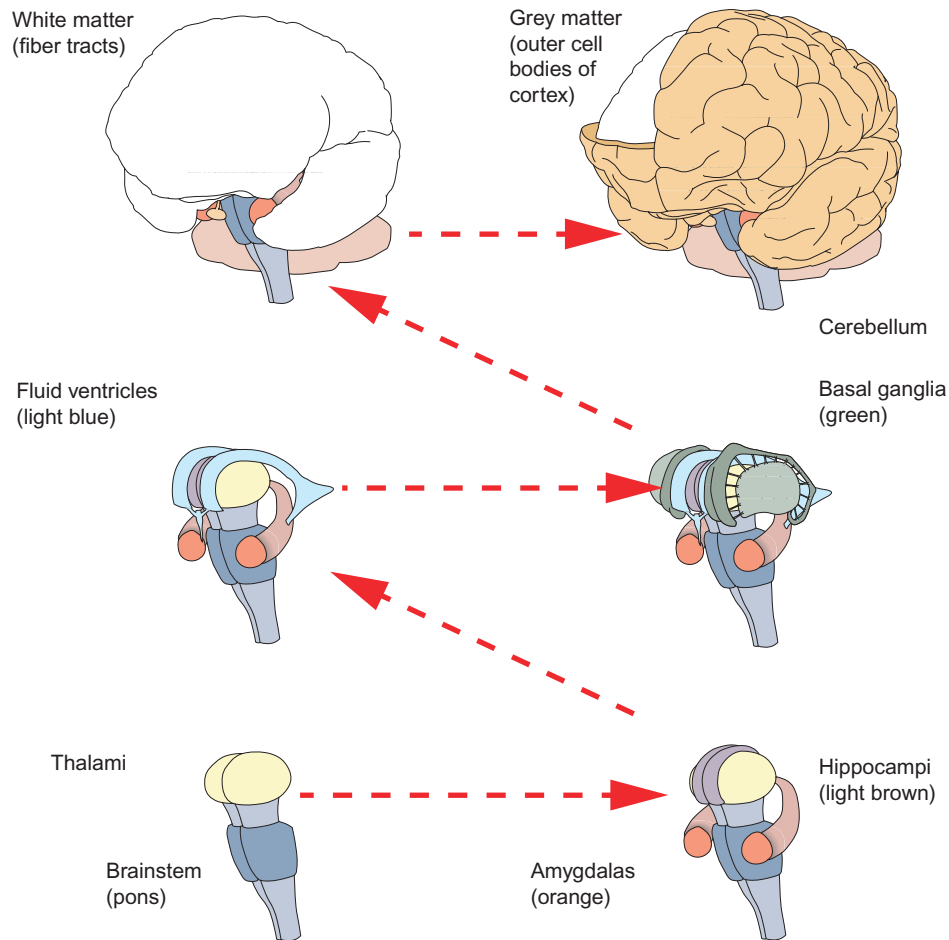


FIGURE 4.9 Growing the brain from the bottom up. If you can memorize these shapes, you will have a solid framework for understanding the brain. Notice how the brain builds on the brainstem, with the thalamus on top as the major input hub. The hippocampi and amygdalae are actually nestled inside each of the temporal lobes. The light blue fluid ventricles have no neurons but provide the brain's own circulatory system. The basal ganglia can be thought of as the output hub of the system. A great deal of traffic flows back to the cortex as well. Source: *Baars & Fu, 2010*.

dialogue with the basal ganglia. Because action control ultimately comes down to doing one thing after another (sequential processes), the basal ganglia (Figure 4.10) are also involved in other kinds of sequential control. A number of theorists believe that the basal ganglia may be involved in a sensorimotor control loop.

The almond-shaped amygdala (Figure 4.11) is a very important hub for memory and emotion, including anger and fear, but also trust and social bonding. You may have noticed that very small structures in the brain can be very important. Very often small nuclei are evolutionarily ancient. The hippocampi and the surrounding medial temporal lobe (MTL) are also vitally important areas of convergence and divergence. Indeed, the brain is full of hubs, like a city with many public squares.

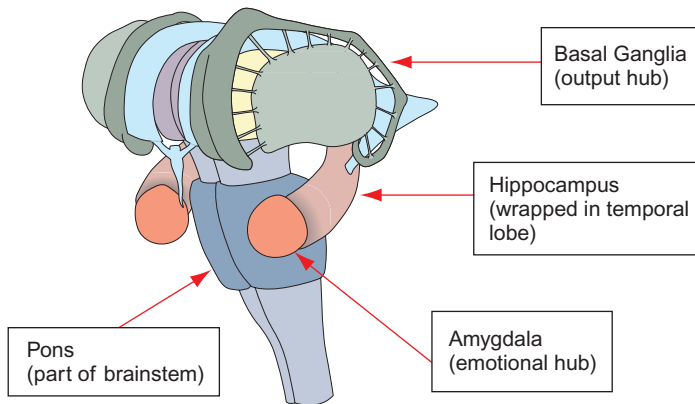


FIGURE 4.10 When the cortex is removed, we see two elegant “shields” on either side of the core brain. These two structures are called the basal ganglia—which means little more than “those big clumps at the bottom,” probably because the early anatomists saw it with the naked eye after removing the cortex. One reason for this unimaginative name is that the basal ganglia do so many things. For our purposes, we will consider it to be the major output hub of the cortex. The light blue structure is not a real structure at all but a pair of fluid ventricles—hollow vessels that carry the internal fluid of the cortex and spinal cord. Source: *Baars & Fu*.

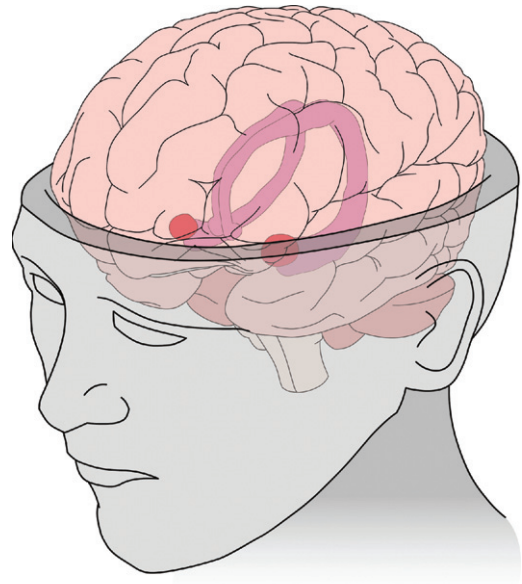
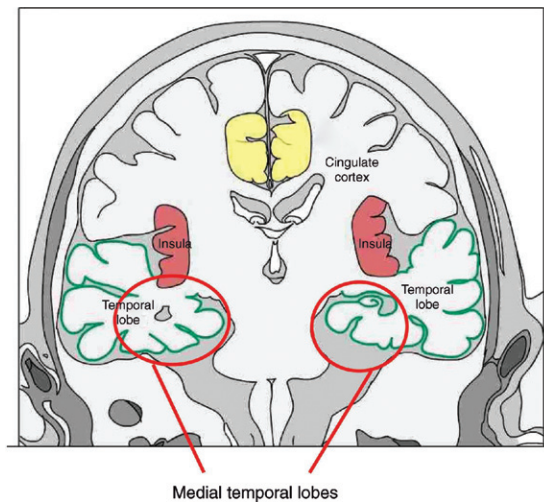


FIGURE 4.11 It’s useful to see the hippocampi and amygdalae from a different perspective. Compare this figure to [Figure 4.11](#). Source: *Baars & Fu*.

The two hippocampi are traditionally called “horns” because they look like upside-down horns. They are part of the ancient smell brain, and therefore they have many functions, including spatial location, navigation, and episodic learning and recall. The two amygdalae, shaped like almonds, are located immediately in front of the point of each horn.

3.1 The thalamus

One level down, in [Figure 4.12](#), we can clearly see the two thalami, egg-shaped structures that are the major sensory input hubs for the cortex. The thalamus is perhaps the second most important structure after the cortex. One reason is that the thalamus and cortex work together so closely that they are often considered to be a single functional system. Notice how the brain builds on the brainstem, with the thalami on top.

[Figure 4.13](#) shows the importance of the thalamus as a gateway to the sensory cortex. [Figure 4.14](#) shows the brainstem in more detail than you may ever have to know. It is provided for the sake of completeness only. In this book we will focus on the cortex and related structures because they are the most important for human cognition. But it would be unfair to ignore the brainstem, which is so important for basic brain and body functions.

As you can see, the brainstem contains cranial nerves that flow in and out of the brain, as well as spinal nerves. It controls vital functions like breathing and heart rate, and it shapes global brain states like sleeping and waking through neuromodulation.

The brainstem is complex and diverse because it is the most ancient part of the human brain. When the brainstem core is damaged, people and animals go into a coma. The

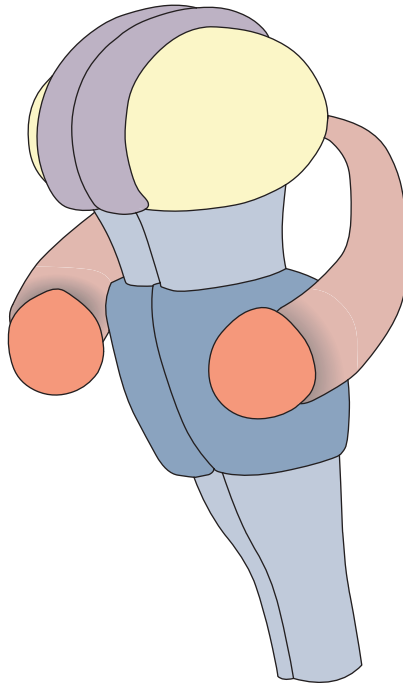


FIGURE 4.12 Notice the two light yellow egg-shaped structures, the two thalami. Although we commonly talk about “thalamus,” it’s understood that there are always two, side by side. Almost every sensory tract stops off at the thalamus before it goes on to the cortex. The thalamus is therefore a natural traffic control center for access to the cortex, and it is believed that in sleep the thalamic gates are almost completely closed. In addition to gating sensory inflow to the cortex, the thalamus interacts with higher regions of the cortex. Source: *Baars & Fu*.

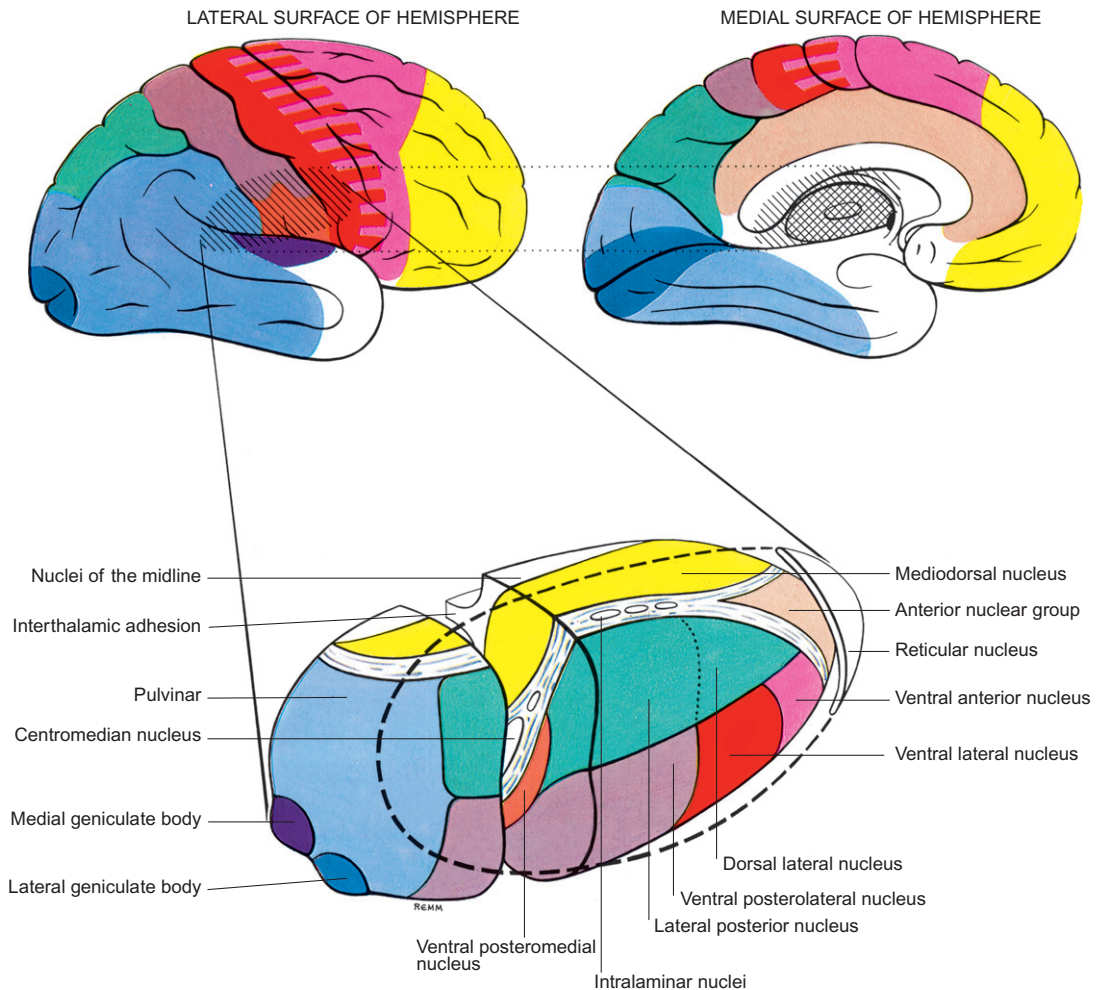


FIGURE 4.13 The cortex and the thalamus: a single unified system. A schematic drawing showing a color-coded mapping of connections from the thalamus to the cortical regions. Source: *Standring, 2005*.

brainstem is therefore believed to contain a fundamental arousal system that develops more levels over evolution.

The brainstem also contains the auditory and the vestibular tracts, as well as the tactile and motor nerves for the torso and limbs. It has vestibular nuclei, which we need to keep our balance when we are walking or sitting, but also simply to see a visual scene in the normal (gravitational) orientation. If you are flying on an airplane that is circling to land, you will see the inside of the passenger cabin tilting as the plane tilts, even if it is dark outside and you have no outside information about your body orientation. Your visual “tilt” comes from the balance

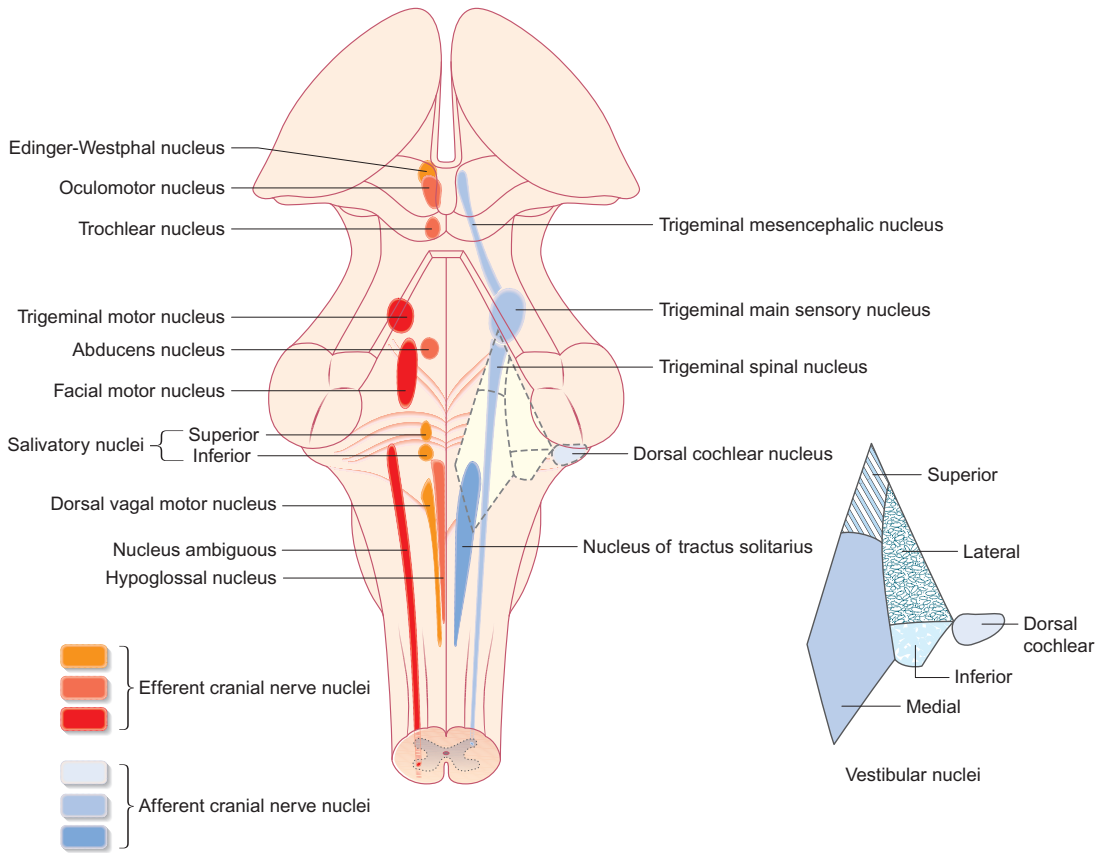


FIGURE 4.14 The brainstem and two thalami seen from the front. Red areas indicate cranial nerves going upward into the brain, while blue areas are cranial nerves flowing downward out of the brain. Most of the nuclei in this figure are not relevant to this book, but you are welcome to try to guess the meaning of *salivatory nuclei*, *facial motor nucleus*, and *oculomotor nucleus*. (Hint: What do you know about motor control of the eyes?) Source: *Standring, 2005*.

receptors in the inner ear. Perceptual orientation is profoundly important. People with impaired vestibular receptors cannot walk or even be moved without feeling dizzy and sick. All animals need to know about the orientation of their bodies in order to maneuver around the world.

The brainstem can be looked at as the root system for the large tree of the brain. It contains more than 40 specialized nuclei (small clumps) of neurons, including some that are involved in neuro-modulation (sending out chemicals for wide distribution to the forebrain). We cannot survive without our brainstem, but this book focuses on specifically human functions, which are generally found in higher regions of the brain.

4.0 SUMMARY

Our aim in this chapter was to provide you with a basic structural map of the brain. The word *cortex* means “bark,” like the bark of a tree. The gray matter of the cortex is only a few millimeters thick. That is where the cell bodies of cortical neurons are located, sending their thin fibers both sideways and downward, toward the hub of the thalamus. Those long (pyramidal) cells eventually join the inner highway system of the cortex. Most of the volume of the brain is filled by those long axons, surrounded by protective white cells, called the “myelin sheath.” Signaling is obviously important to the brain, since so much tissue volume is dedicated to the thin branches that connect nerve cells.

While the brain has separable parts, like the two hemispheres and the four major lobes, every part is highly interconnected with the others. That is especially true for the cortex and thalamus, the great input hub of the cortex. The basal ganglia may be regarded as an output hub to the motor pathways that control our muscles.

Some important points to remember are that the brain has evolved over time, so lower structures are often more ancient in origin than the top levels. Nevertheless, these lower structures are also functionally vital. The brainstem controls breathing and heart rate, without which we could not live.

The neocortex represents mammalian developments, and the frontal lobes have expanded their size when compared to other primates. The frontal lobes are sometimes called “the organ of civilization” because they support the basic ingredients of human cultural development, including language.

5.0 STUDY QUESTIONS AND DRAWING EXERCISES

5.1 Study questions

1. What is the cortex? Why does it look the way it does?
2. What are the four major lobes of the cortex and what are some of their functions in human cognition?
3. Where is the medial temporal lobe located? What are some important parts?
4. Briefly describe the role of the thalamus.
5. How are the two hemispheres linked? Are there any differences in how they function?
6. What are some functions of the basal ganglia? The brainstem?

5.2 Drawing exercises

1. Label each part in [Figure 4.15](#) from the top to the bottom.
2. Label the parts in [Figure 4.16](#). Refer to the figures in the chapter if you need to.

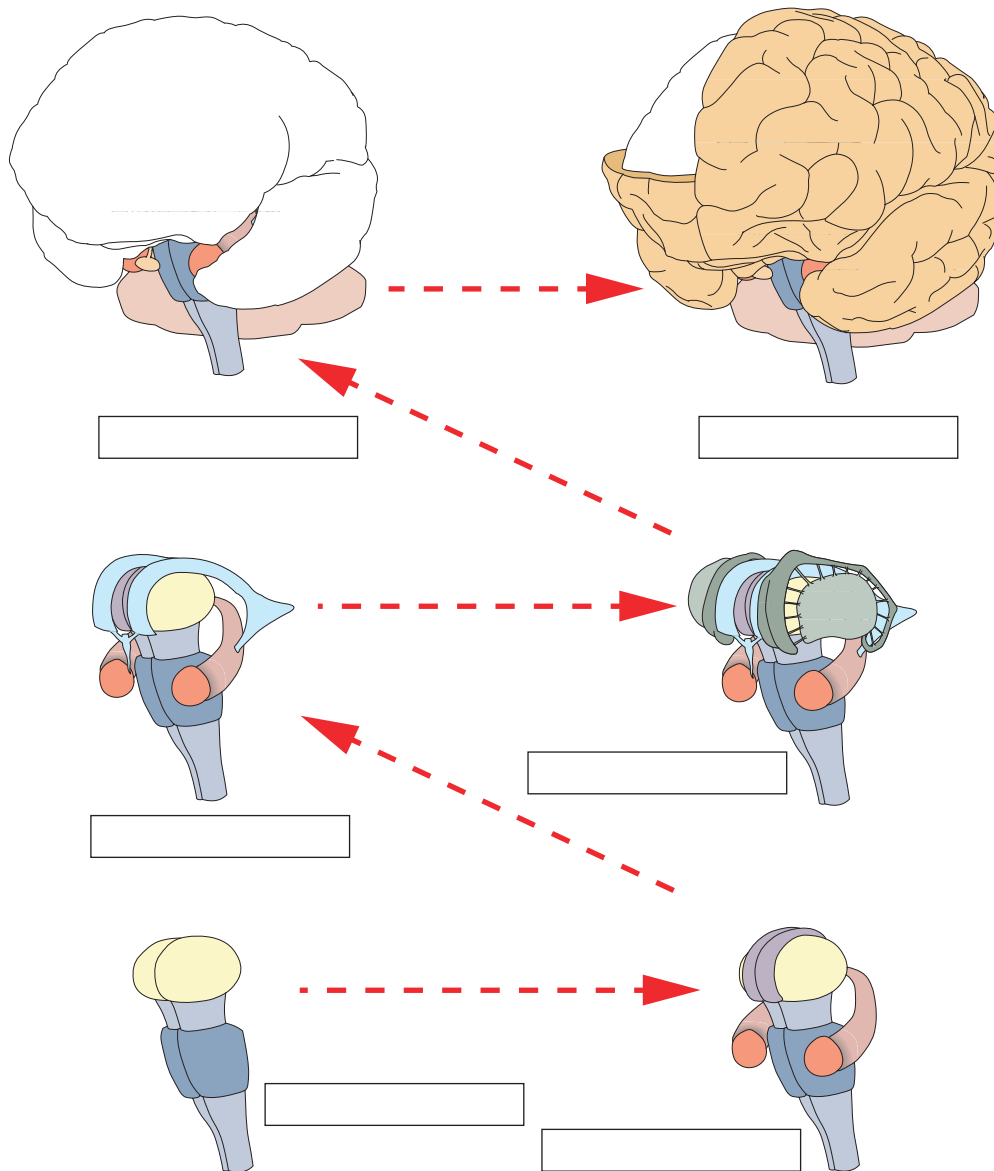


FIGURE 4.15 Label each part of the figure. Source: Baars & Fu.

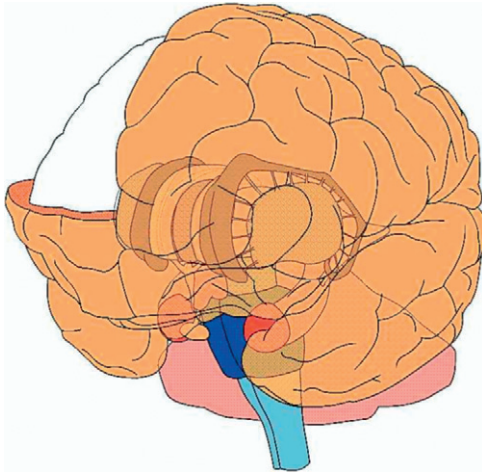


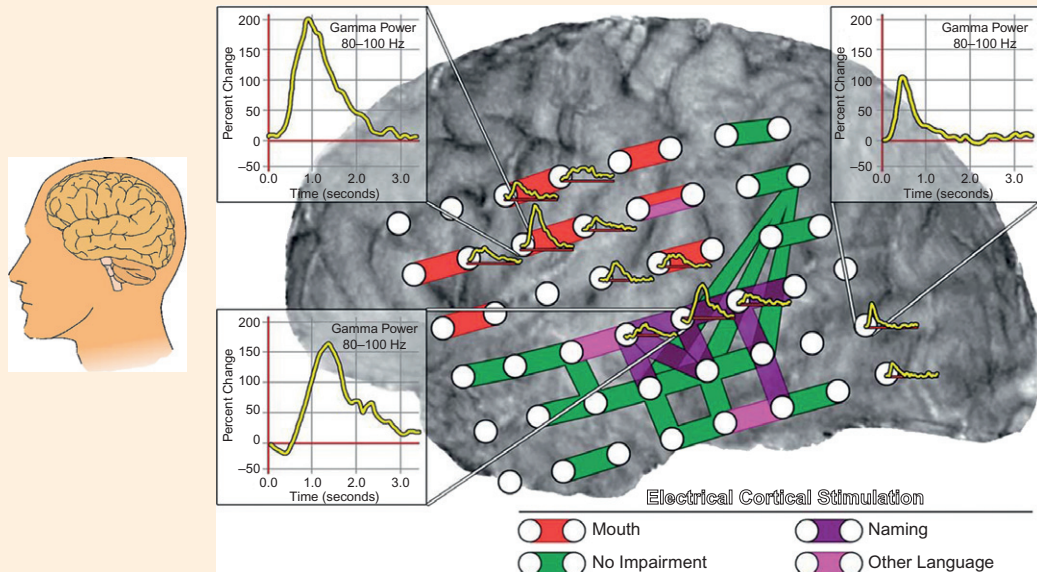
FIGURE 4.16 Label each part of the figure. Source: *Baars & Fu*.

Brain imaging

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LISTENING TO THE BRAIN



Direct electrical recording and stimulation of the left hemisphere of a waking patient. The patient feels no pain because the cortex has no pain receptors, and the incision is protected with local anesthesia. It is important for the patient to be conscious during exploratory surgery to help locate vital functions that must be protected. Notice that the surgeon has labeled electrodes for the mouth (white dots with red stripes) and for picture naming (dark purple stripes). The three graphs show the averaged electrical activity over three seconds after the patient is shown a visual object to name. Gamma activity (80–100 Hz) peaks the fastest in the posterior site, then near the motor cortex (red), and finally in the upper temporal lobe (purple). Can you guess why?

Source: Crone *et al.*, 2006.

1.0 INTRODUCTION

The ability to directly observe the living brain has created a scientific turning point, much like Galileo's first glimpse of the moons of Jupiter. Humans have studied the sky for many centuries, but when glass lenses and telescopes were invented, the pace of discovery took off. But just as Galileo's telescope required constant improvement, our "brain scopes" have their limits. We should know their limits as well as their capabilities.

A perfect brain observer would keep track of tens of billions of neurons many times per second. The perfect observer should then be able to track the shifting interplay between groups of

neurons, with thousands of signals traveling back and forth. By analogy, a perfect spy satellite would see every human being on Earth as well as all the things we say to one another.

Such a perfect observer does not exist. We are more like distant space explorers beginning to observe a new planet. We pick up signals without knowing exactly where they come from, whether they are made by living creatures, what languages they speak, or even whether the signals mean anything.

We know that the brain has major pathways and maplike arrays of neurons and that single spikes as well as waves (oscillations) can travel between brain maps. Brain oscillations vary between 0.5 to 120 Hz (i.e., up to about 120 cycles per second), with occasional faster events. If we add in the neurotransmitters and neuromodulators that shape signal transmission, the potential number of signals is enormous.

Neurons have *electrical*, *magnetic*, *chemical*, and *anatomical* properties. Each of these can be measured. As you know from [Chapter 3](#), every neuron can send a fast electrical signal down its axon. We can record this activity in the cell or in the surrounding fluid. The brain also has a rich fuel supply, and when a specific region of the brain is working harder, it needs extra fuel. Those facts give us all our brain measurement techniques: neurons, and networks of neurons, generate electrical and magnetic signals. Metabolic processes can be picked up using methods like PET and fMRI. The anatomical shape of brain structures can be detected by CAT scans and MRI. As a result, we can now see functional brain activities for speech, action control, motivation, sensory perception, and more.

1.1 Basics

Brain imaging has been a breakthrough technology for cognitive neuroscience, building on decades of cognitive psychology, behavioral conditioning, psychophysics, and brain science. Before imaging techniques matured, our knowledge came from animal studies and the hap-hazard injuries incurred by human beings. But brain injuries are extremely imprecise, and to locate the damage, neurologists often had to rely on postmortem examination of patients' brains—as in the case of Broca's and Wernicke's patients. The brain can often compensate for damage, so lesions change over time as cells die and adaptation occurs. Therefore, post-mortem examinations do not necessarily reflect the injury at the time of diagnosis. Animal studies depend on presumed homologies—similarities across species—that were often not convincing. No other animals have language and other human specializations. It was therefore very difficult to understand how brain functions in animals mapped onto human cognition.

Today, we have perhaps a dozen techniques that are rapidly becoming more precise. Medical needs often drive this expensive technology because it applies to many organs in the body. As a result, we now have ways to study the distribution of billions of neurochemical receptors in the brain, the thickness of cortex, the great highway system of white fiber bundles, and, most important for cognitive neuroscience, the *functional* activity of the brain—the basis of its adaptive capacities. New advances are allowing scientists to investigate not only specific brain regions but also the dynamic pattern of connectivity between them. Some of the massive “wiring” of the brain is shown in the figure, but like the World Wide Web, the wiring

is only part of the story: ever-changing connections are being made that can alter in a fraction of a second.

1.1.1 Accuracy in space and time

Figure 5.1 shows today's methods and their accuracy in space and time. (See Chapter 1 for the spatial and time magnitudes of the brain.) Techniques like functional magnetic resonance imaging (fMRI), which records metabolic changes like blood oxygenation, have good spatial resolution and relatively poor time resolution. fMRI has a response time of about six seconds because the fMRI signal (called the BOLD signal) reflects a flow of oxygen-rich blood traveling to "hot spots" that are doing extra work. The changes in blood flow take several seconds to catch up with the neuronal activity. fMRI is therefore too slow for tracking single neurons and populations in "real time."

We do not have a complete census of all the neurons in the brain the way a human society might conduct a census of the whole population. We are always sampling from a very large set of active neurons. For that reason we cannot be sure that we know every single cell type in the brain, down to the smallest level. Brain anatomists are constantly discovering new specialized neurons in some local neighborhood. For example, the light receptors that adjust our body to sunlight and darkness were only discovered in recent years.

fMRI has very good spatial specificity compared to electroencephalography (EEG) and magnetoencephalography (MEG), which use electrical and magnetic signals, respectively.

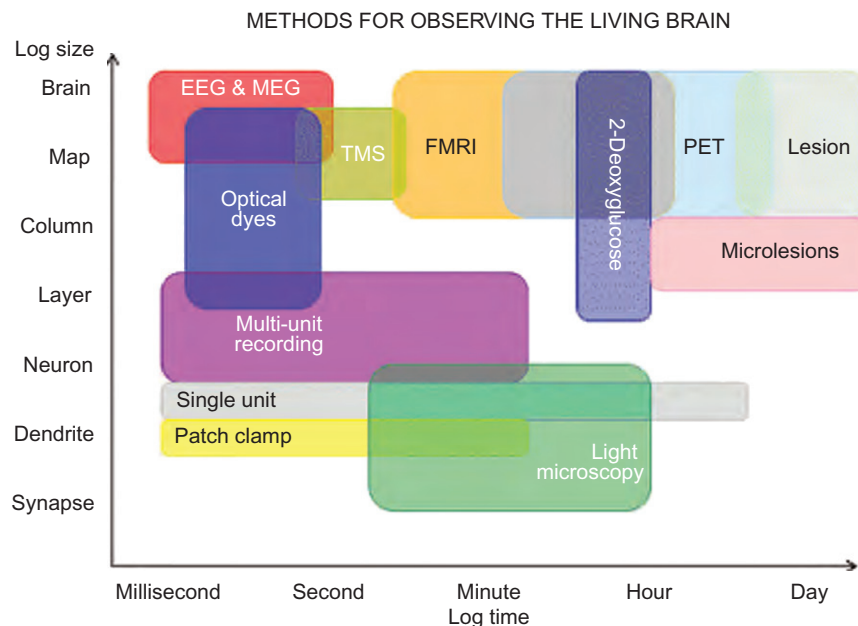


FIGURE 5.1 How good are current methods? Pros and cons of imaging techniques: differing imaging modalities have different resolutions. While some approaches have a very high temporal (time-based) resolution but a low spatial (space-based) resolution, other modalities have an opposite relation.

Thus, fMRI is used to localize brain functions. But EEG and MEG have excellent temporal resolution—almost instantaneous—and relatively poor spatial precision. They can track neuron population activity as quickly as tens and hundreds of milliseconds, but it is hard to know *which* set of neurons is doing it. fMRI is sometimes used in combination with EEG to obtain the best temporal *and* spatial precision. Combined measures may give us the best of both worlds.

1.1.2 A brain in a shoebox: coordinates

When sailors learned to draw imaginary lines of latitude and longitude to place a coordinate system around the earth, it became possible to specify any place with a precise “x” and “y” number. The earth’s coordinate system became a major advance in navigation.

The shape of the brain is more complex than the earth’s, but the strategy of placing it in a three-dimensional space is the same. Scientists can specify a precise location in the brain by placing it in a virtual shoebox so each point in the brain has a unique address in three orthogonal dimensions. Each point can be specified as x , y , and z . The best example is the Talairach Coordinate System illustrated in Figure 5.2.

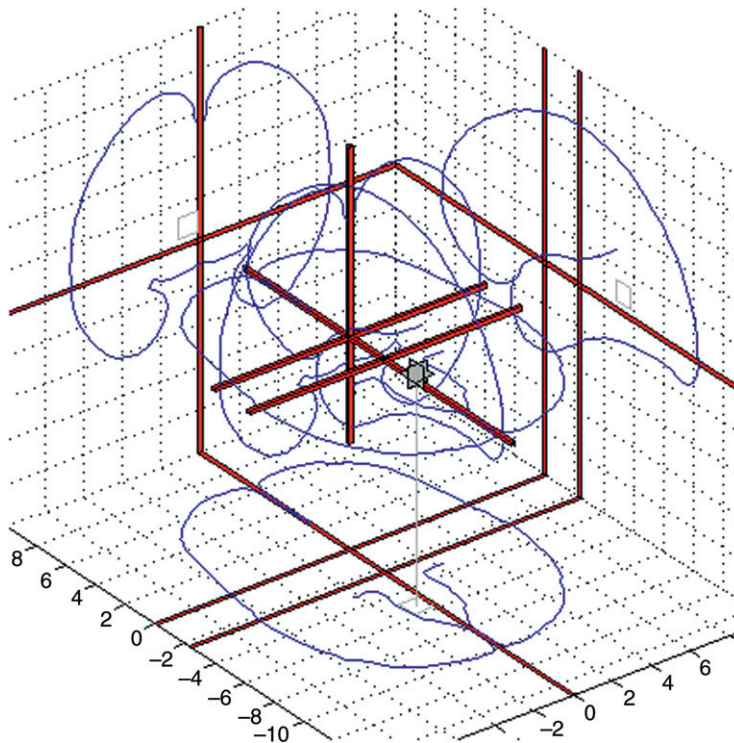


FIGURE 5.2 A coordinate system for the brain. The brain is typically imaged in three dimensions: axial, sagittal, and coronal (see Chapter 1). Putting the brain together into a three-dimensional image allows the coordinates to be determined across these three dimensions. Source: http://neuroinf.imm.dtu.dk/old_brede/WOROI_96.html

Different people have different brains. Just as our heads have distinctive shapes, so do the organs inside. We begin to lose neurons after birth, so infants have more neurons than older children, teenagers, or adults. On the other hand, brain myelination (the wrapping of long axons by white protective cells) keeps growing until about age 30. Serious illnesses, growth and aging, learning and exercise, brain injury, and even malnutrition can add or subtract tissue. The brain keeps changing.

Individual brains therefore need individual images. MRI and CAT scans are used to take a snapshot of the three-dimensional brain at any particular moment. Figure 5.3 shows the smallest unit imaged using MRI: a “voxel.” Figure 5.4 shows a brain navigation program with a screenshot of the standard coordinate system used in most MRI research.

Brain surgeons need to know where to remove disease-causing tissue and which regions need to be left untouched. Structural images from MRI and CAT scans give us a three-dimensional map of the brain. But maps are also essential for understanding functional measures, like EEG, MEG, fMRI, and deep brain recording. Typically, measures of brain structure and function are combined.

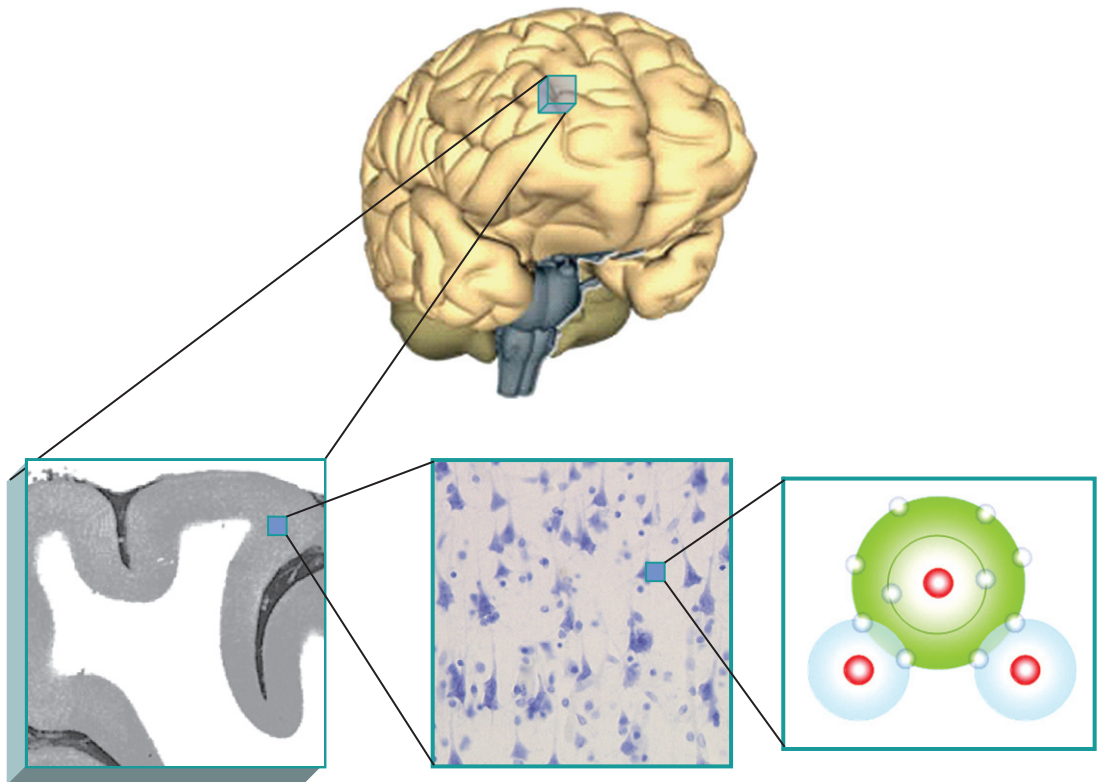


FIGURE 5.3 A single “voxel” gives the smallest unit of volume. The voxel is a representation of a volume in three-dimensional space. In the brain, the resolution of the MRI scanner determines how small the voxels can be. Higher magnetic field strength increase the spatial resolution and thus the ability to represent separate structures in the brain. Source: Jones *et al.*, 2002.

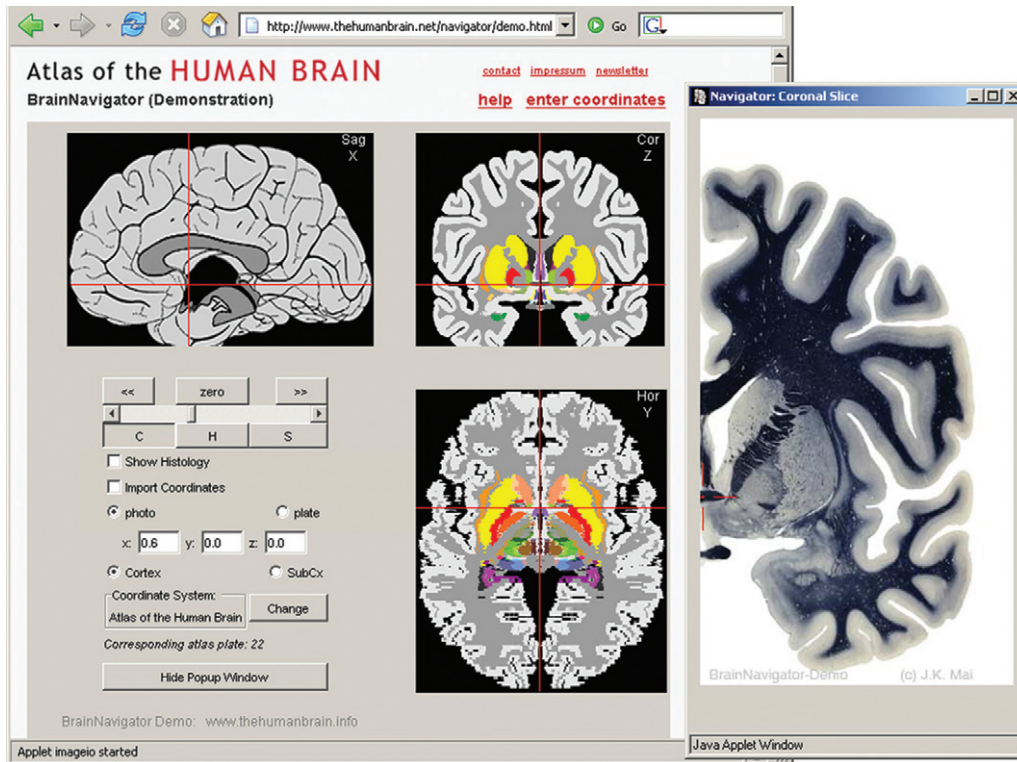


FIGURE 5.4 Brain navigation software allows the user to translate precise locations into conventional brain locations in order to compare results across patients. Notice the orientation of the standard slices. The x, y, and z coordinates are known as the Talairach system (Talairach & Tournoux, 1988). Anatomical landmarks like the corpus callosum can be seen in the upper left display. Source: Talairach & Tournoux, 1988.

1.2 Single neurons

Even with fast-improving imaging techniques, the most direct evidence about the living brain still comes from *intracranial* electrical recordings. One reason is that the electrical voltages in the brain are much greater than on the scalp—on the order of *millivolts* rather than *microvolts*. Surface EEG is filtered through a watery medium of brain tissue, skin, bone, and muscle. When you frown, the muscles above your eyes contract, and thin layers of muscle across the scalp stretch and adjust. Even eye movements have large effects on the scalp-recorded EEG. Thus surface EEG recordings mix many electrical sources, as well as being filtered through layers of tissue. About 99.9 percent of the signal strength is lost.

Direct brain recording therefore has a great advantage. The biggest drawback is that it requires invasive surgery. In humans it is never done without medical justification. However, many animal studies use direct brain recording, and these still provide much of the basic evidence.

Wilder Penfield and his colleagues pioneered electrocorticography (ECoG) in humans in the 1950s. Epileptics with uncontrolled seizures can benefit from surgical removal of seizure-causing

scars in the cortex. ECoG recordings can show where such “epileptogenic foci” are located. In addition, the surgeons need to know which areas to avoid damaging because they are vital for perception and language. ECoG exploratory studies are relatively safe and practical. Probing the cortical surface is generally pain-free because the cortex does not have pain receptors. The scientific benefits have been very important. ECoG studies in conscious humans are helping to uncover the neural basis of language, conscious perception, and voluntary control.

1.2.1 Recording and stimulating neurons

Single neurons have electrical and magnetic properties, like electrical batteries. We can measure the charge left in a battery and the amount of work it can do for us. We can also measure its magnetic field, as well as its chemistry and overall structure. Hubel and Wiesel (1962) recorded single feature-sensitive cells in the visual cortex of the cat—an achievement for which they received a Nobel Prize in 1981. More recent work has recorded in medial temporal lobes (Figure 5.5). Like every method, electrical recording of axonal firing has its limitations, but it continues to be a major source of information.

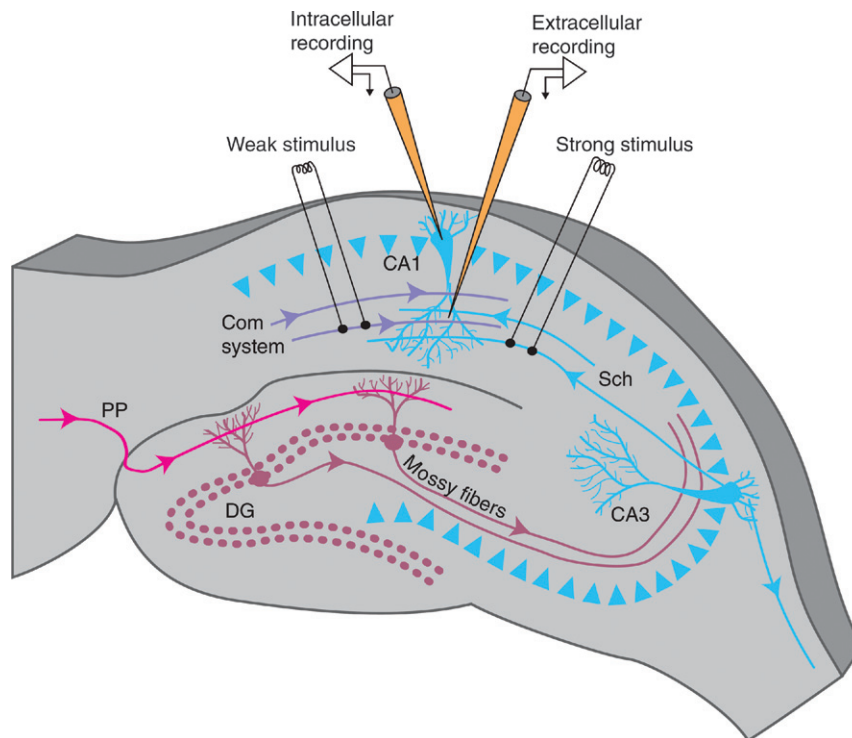


FIGURE 5.5 The voltage and current flow of neurons have been studied using microelectrodes inserted in the cell, compared to a reference electrode placed outside. Large numbers of neurons also generate electrical and magnetic fields, and because many neurons are lined up in parallel arrays, like vast fields of wheat or corn, their overall electrical and magnetic fields “point” in a consistent direction. Source: *Squire et al., 2002*.

Neurons fire a maximum of 1,000 Hz, but cortical neurons average about 10 Hz. We have no “universal census” of cortical neurons, so we do not know with certainty how representative the small samples we observe really are.

In many countries, deep electrode recordings are allowed in primates, such as the macaque monkey, under suitable ethical constraints. The macaque brain has some striking similarities to human brains. Single-neuron recording in the macaque prefrontal cortex may show working memory. In a typical experiment, a macaque is trained to fixate visually on a cross on a computer screen and to perform a delayed response to a visual stimulus. The animal is trained to wait for a moment before looking in the direction where a stimulus appears or, alternatively, to look in the opposite direction. We can then record the activity of a single prefrontal neuron in the three phases: the presentation of a visual stimulus, the period when the monkey keeps the location of the visual stimulus in working memory, and the response of looking in the opposite direction.

1.2.2 Single neuron recording in humans

Some of the most astonishing findings in the last ten years have come from single cell recordings in humans. This is ethically possible only when there is a medical necessity for the risks of surgery, like infection and brain damage. However, the technology for safe and effective epileptic surgery has been worked out over half a century.

Depth electrodes have been used in humans. Typically, these electrodes are implanted before surgery in a patient who has otherwise untreatable epilepsy. The implants can determine where epileptic foci begin at the onset of a seizure and where critical regions of the brain are located that must not be lesioned.

While a single cell cannot tell us much about human cognition, a recent experiment provided some intriguing results regarding conscious and unconscious visual perception (Figure 5.6). While the spiking neuron is a plausible unit of brain activity, some scientists believe that graded dendritic currents in each neuron may do useful information processing; some argue for subcellular processes inside the cell; others point to nonclassical cells and synapses; and many scientists believe that real brain processes only take place at the level of *populations* of neurons. Therefore, recording axonal spikes is important, but it may not be the only important thing going on. Obviously, it’s a risky business to jump from a single neuron to more than 10 billion in the vast forest of the brain.

2.0 ELECTRICAL AND MAGNETIC FIELDS

The brain has billions of neurons lined up more or less in parallel. The long pyramidal neurons of the cortex mostly point their axons inward to the thalamus, and later many axons join the great hubs and highways of the inner white matter. However, pyramidal cells have input dendrites that are mostly spread out horizontally, following the curve of the cortex. When pyramidal neurons fire a spike down the axons, their dendrites also change. Those flat and bushy horizontal “arbors” of dendrites are picked up as EEG activity at the scalp because their electrical fields happen to point outward.

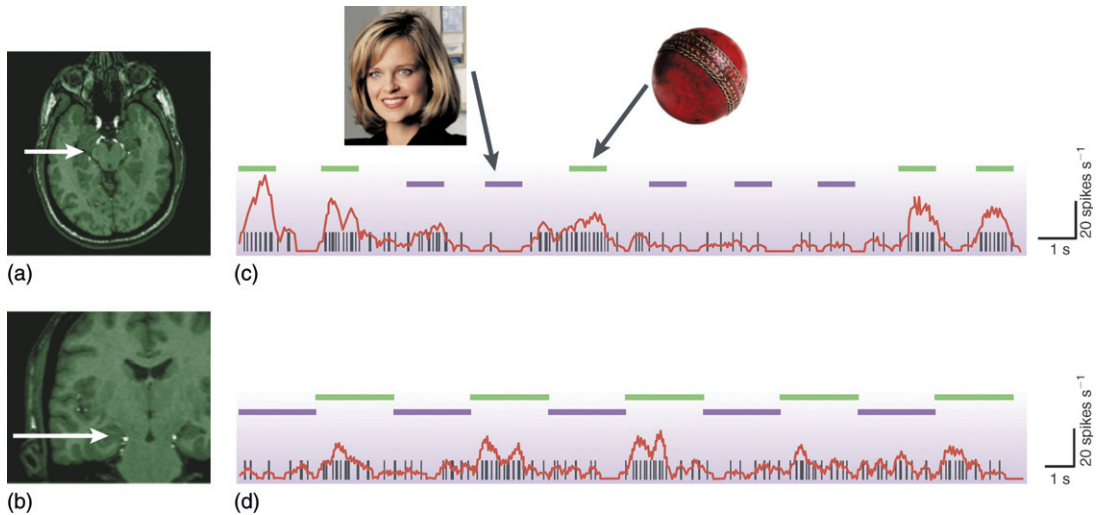


FIGURE 5.6 Single neurons reflecting conscious perception. A remarkable experiment in which both conscious and unconscious stimuli were shown simultaneously to two different eyes using a variant of binocular rivalry (see Chapter 6). In the upper row (c), the woman's face is conscious, but the ball is not; in the lower row (d), this is reversed. Peak firing rates, in red, during the time periods marked by the green horizontal bars, when the subject is reporting that the woman's face can be seen. The brain seems to determine which of the two simultaneous stimuli will become conscious when the signal reaches the object recognition areas in the cortex. The electrode locations are shown on the brain scans on the left (a, b). Source: *Rees et al., 2002*.

All streams of electrons generate both electrical and magnetic fields, which radiate at right angles to each other (Figure 5.7). Therefore, we can also pick up the brain's magnetic field—at least those components that conveniently point outward from the scalp. Most the field strength in the brain is not measurable from the outside. We just take advantage of radiating fields that can be picked up.

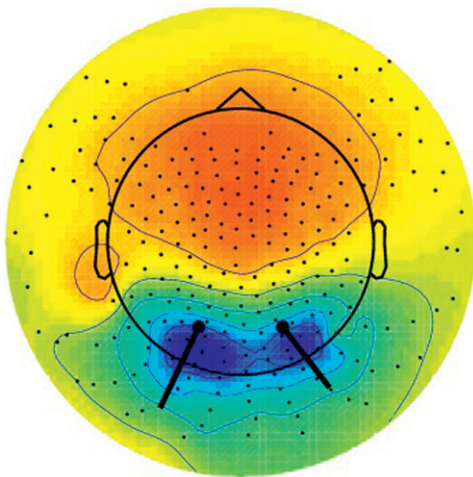


FIGURE 5.7 The brain radiates electrical and magnetic fields. Here is an example of a 252-channel EEG recording. The head is shown from above, with the front of the face on the top of the figure and the back of the head on the bottom. Dipoles are shown in black arrows, and their centers are shown in blue. Based on these data, what part of the brain do you think is active? Source: *Schwartz Center for Computational Neuroscience* (<http://sccn.ucsd.edu/eeqlab/comp252.html>), with permission.

2.1 Electroencephalography: the electrical fields of the brain

Scalp EEG is a standard tool in medicine. When an accident victim comes into an emergency room with a head injury, scalp EEG is one of the first tests. With only 21 electrodes, a great deal can be observed, including gross brain damage, coma and stupor, sleep, waking, epileptic signals, and more. Computer programs for analyzing EEG are constantly improving.

The biggest difficulty in scalp EEG is locating the source of the recorded signal. The brain is a large, wet medium, and recording from the scalp results in a loss of 99.9 percent of the source. This is like trying to understand a watery planet where all the radio signals come from deep in the ocean and most of the signal power is lost before the satellite can pick it up.

The brain's electrical activity can be recorded through the scalp or on the surface of the cortex. Rather than picking up electrical activity direct from neurons, the electroencephalogram picks up the electrical field. The resulting record is an *electroencephalogram* (EEG). The EEG was discovered in 1929 by Hans Berger.

EEG is a relatively direct measure of the brain's electrical activity. But with tens of billions of cortical neurons firing about 10 Hz, we have several trillion electrical events per second. The raw EEG was therefore difficult to interpret before the advent of powerful computerized analysis.

However, when the EEG is averaged over a number of trials and “locked” to a specific zero point, like the onset of a stimulus, the averaged electrical activity yields elegant and regular waveforms. This event-related potential (ERP) is sensitive to large population activity that characterizes visual, auditory, and even semantic processes.

The brain can also be *stimulated* with electrical and magnetic energy. Today we can stimulate deep brain regions using microelectrodes, which are sometimes useful for treating severe depression and Parkinson's disease.

2.2 Analyzing the electroencephalogram

While the brain has about 100 billion cells, the cortex is now believed to have about 1,000 specialized regions, originally discovered by Brodmann (1909) and therefore still called Brodmann areas. They are the postal codes of the brain. Other major structures, like the thalamus, have their own regional organization.

Humans communicate by phone, radio, and television. Those techniques use different coding schemes, often with different waveforms (such as AM and FM radio). The brain seems to have many coding schemes. The visual cortex, for example, has “visuotopical maps”: two-dimensional arrays of the visual input that begin with the retina and continue in the visual cortex with area V1. Higher-level maps have more abstract visual representations, like motion, color, faces, houses, and other objects. Since these arrays often correspond to one another, they are said to be “topographically mapped.” A particular point on the retina, like your center of visual gaze, corresponds to the same point in the thalamus, V1, and higher visual maps. This is a *spatial* coding scheme, like a video camera or a computer screen.

The waveforms in [Figure 5.8](#) show major bands (ranges) of waves in the EEG. These oscillations are believed to play important roles in the brain (See [Box 5.1](#) for an interesting experiment using these EEG measures.). Notice the top oscillations, which represent “raw” (unprocessed) EEG, recorded from any electrode on the scalp. During the waking state, these oscillations look nearly random, as if they are generated by chance events. For that reason EEG was controversial for many years, until the emerging evidence showed that the choppy “ocean” of the brain consists of many regular waveforms ([Figure 5.9](#)).

When random snippets of EEG are averaged, the result is a straight line, since random positive and negative oscillations add up to zero. This fact is used in the event-related potential, discussed in the following.

The activity of large populations is another important level of analysis (Freeman, 2004; John, 2001). Spontaneous EEG shows different patterns of activation. For example, during deep sleep, the raw EEG shows large, slow waves. This indicates that large groups of neurons are synchronized on a very large scale throughout the brain. When the subject wakes up, this slow pattern is replaced by small, rapid electrical waves, indicative of rapid and



FIGURE 5.8 Regular rhythms in different parts of the brain are shown. A method called Fourier analysis allows us to decompose the density (or power) of regular waveforms that are buried in noisy EEG recordings. The graphs show the resulting power curves. The colors correspond to different frequency ranges. Source: Zoran Josipovich, with permission.

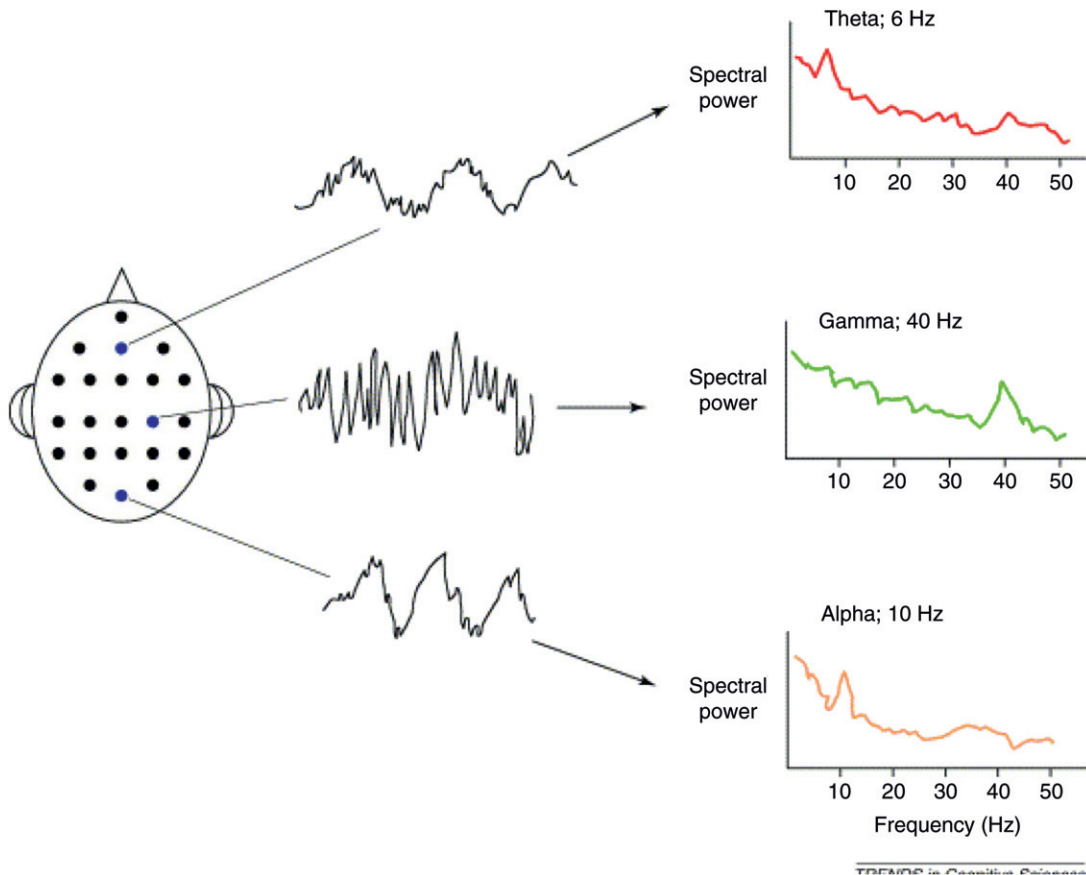


FIGURE 5.9 Some power spectra showing peaks at canonical EEG frequencies. Although any of the frequencies can occur at any electrode site, alpha power is often recorded at posterior sites, theta at frontal sites and gamma over sensory cortex. Source: *Ward, 2003*.

flexible information patterns of interaction in the brain. It is currently believed that cortical neurons do not fire at different rates during deep sleep compared to waking, but rather that waking EEG allows a far greater amount of interactive processing. Sleep is not a passive state, but a different operating mode of the brain, with its own functions. One of these is believed to be the consolidation of memories based on waking experiences (Hobson & Stickgold, 1995).

EEG has a millisecond time resolution, but its spatial resolution is rather poor. It is very difficult to locate the electrical source of the EEG signal. It helps to increase the number of electrodes and to use sophisticated analytical methods. However, EEG gives us little information about brain regions deep beneath the cortex.

2.3 Averaging the EEG

It makes sense to get the average annual income in a country. One reason is that there is variability between the poorest and wealthiest people. Another is that it helps to have one number to describe millions of people. The point of statistics is to simplify very large numbers to just a few. A similar approach works with the electrical activity of the brain, using the “event-related potential” (the word *potential* means “voltage”). Event-related potentials (ERPs) were discovered several decades ago, before high-speed computers were available to analyze the EEG. When a bright flash or a loud sound is presented to an animal or a human being, a wave of activity travels throughout the cortex and thalamus. That brain activity is “evoked” by the flash or the bang, and it is helpful to show the results starting with the moment of the stimulus. The evoked (that is, they occur in response to the event, in this case a flash or bang) potential waveforms are reflected in the EEG, but they tend to be swamped by other brain activity, much like a giant wave in the ocean that is invisible as long as it is swamped by other wave activity in the sea.

As just pointed out, the irregular or “random” component of the EEG drops out when multiple stretches of the signal are added up or averaged. However, the large and distinctive signals of the ERP do not drop to zero. Rather, they add up over each trial, showing up as the event-related potential (ERP). ERP peaks and valleys are quite regular and stable over time. They are believed to reflect large neuronal populations that are triggered by the input.

When we average over a number of half-second stretches of EEG, we obtain the ERP in [Figure 5.10](#). EEG reveals brain patterns during sleep and waking, abnormalities during diseases like epilepsy, and even the brain areas that respond to music. A more recent technique, magnetoencephalography (MEG), is related to EEG and has provided new ways to image the human brain.

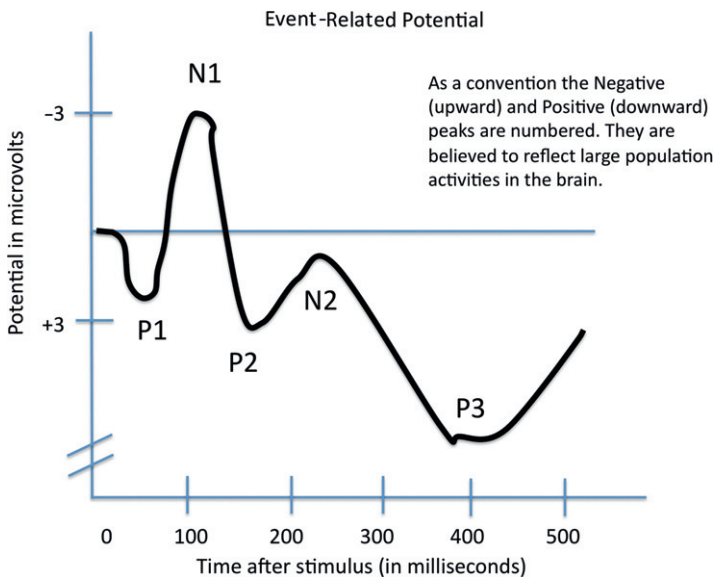


FIGURE 5.10 While the EEG is complex and irregular, averaging the EEG trace over multiple presentations of a stimulus reveals a remarkable degree of regularity, as shown in this event-related potential (ERP). Although the ERP is not completely understood, it appears to reflect large, successive neuronal population activities in the cortex and related structures. The timing and size of the major peaks and valleys are sensitive to many cognitive and emotional factors, including surprise. Similar averaging methods are used with other brain recording methods such as MEG. Source: *Baars*.

BOX 5.1

THE EEG OF MEDITATION

A study by Lutz *et al.* (2004, see Figure 5.11), using EEG, focused on the brain activity of experienced Buddhist meditators. EEG signals were recorded in expert meditators and control subjects during normal rest and during different stages of meditation. Three stages were used: rest, meditative state, and a pause stage between meditative states. Lutz *et al.* found that, during meditation, the group of experienced meditators had a dramatically higher level of gamma-band oscillations. The researchers

also found long-distance phase synchrony between frontal and parietal areas in the brain. From these results, Lutz *et al.* speculate that meditative training enhances the integration of distant brain areas. Interestingly, the results showed that brain activation even at rest differed between the expert and naïve groups. This indicates that substantial meditative experience can alter the workings of the brain, although at present we can only speculate at the precise cause and effect relationships.

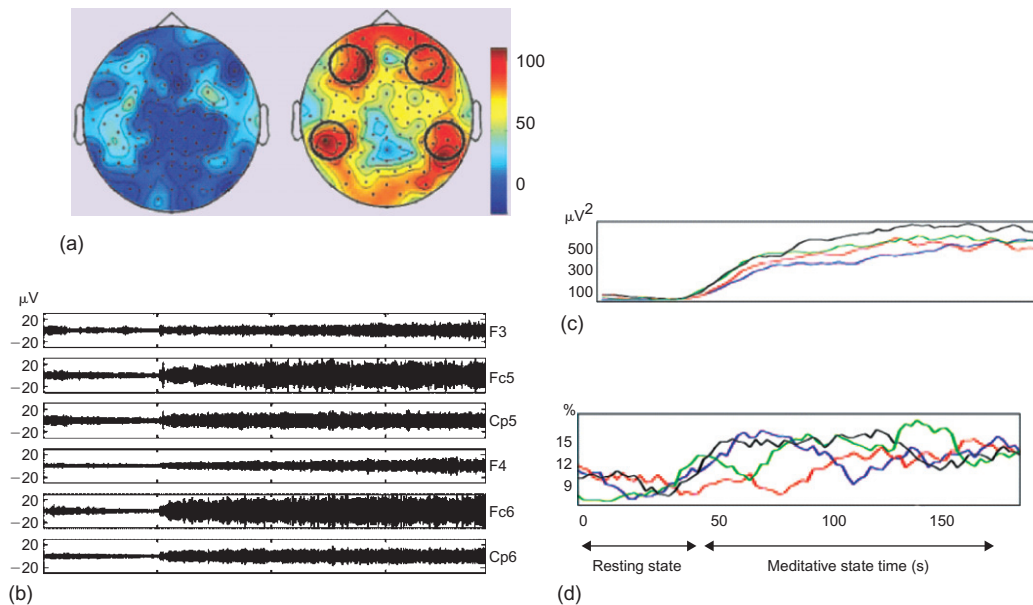


FIGURE 5.11 Measuring the effects of meditation: the study of Lutz and colleagues (2004) shows that gamma power is much higher in practicing meditators (right) compared to non-meditating controls (left). The color scale indicates the percentage of subjects in each group that had an increase of gamma activity during the mental training. Source: Lutz *et al.*, 2004.

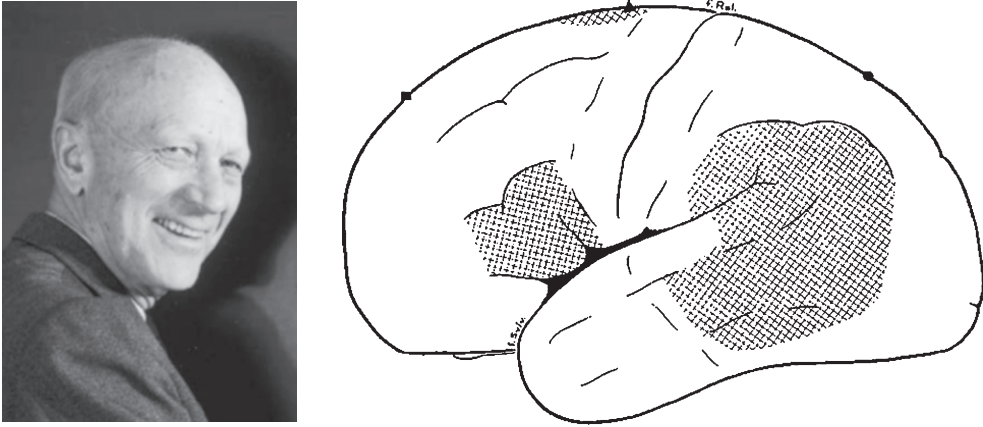


FIGURE 5.12 Left panel: Wilder Penfield. Penfield and colleagues devised open-brain neurosurgery for untreatable epilepsy in the 1950s. Right: Penfield's map of brain regions where electrical stimulation interferes with language. Notice how closely these regions correspond to the classical Broca's and Wernicke's patients studied a century before. Sources: *Adelman & Smith, 2004*.

2.4 Stimulating the brain

What if you could evoke neural activity in a safe fashion? Such a method would be especially useful to test causal relationships between neural activity and cognitive functions. Early work on direct electrical brain stimulation began with Wilder Penfield, a neurosurgeon at the Montreal Neurological Institute ([Figure 5.12](#)). Penfield and his colleagues treated patients with intractable epilepsy. In open brain surgery, patients can remain awake and responsive, since only local anesthetic is needed at the site. There are no pain receptors in the brain itself, so the cortex brain can be operated on without general anesthesia.

2.4.1 A safe way of interfering with brain function: transcranial magnetic stimulation (TMS)

It is now possible to stimulate brain lesions in healthy subjects. Without cutting a person's brain, we can alter the brain's level of activity locally. Brief magnetic pulses over the scalp either inhibit or excite a region of cortex. For example, if you stimulate the hand area of the motor cortex, the subject's hand will move and twist. Applying an inhibitory pulse over the same area will cause subjects to have difficulty moving their hands. This is called *transcranial magnetic stimulation* (TMS) or, as one leading researcher called it, "zapping the brain" (Cowey & Walsh, 2001). TMS appears to be generally safe. By applying TMS, we can test causal hypotheses about the contribution of specific brain regions to cognitive processes. Since the TMS works at the millisecond scale, it is also possible to study how rapid waves of processing develop. Recent TMS studies emphasize that magnetic pulses rarely have simple, local effects. Rather, like other kinds of brain stimulation, magnetic pulses often trigger off widespread activities, depending on the subject's expectations and ongoing goals.

2.5 Magnetoencephalography: magnetic fields of the brain

Magnetoencephalography (MEG) measures the magnetic field produced by electrical activity in the brain (Figure 5.13). Its spatial resolution is now approaching a few millimeters, while its temporal resolution is in milliseconds. Because of the physics of magnetism, MEG is highly sensitive to dendritic flow at right angles to the walls of the sulci (the cortical folds). MEG results must be superimposed upon a structural image of the living brain. MEG uses a process called *magnetic source imaging* (MSI) to coregister the magnetic sources of brain activity onto anatomical pictures provided by MRI. MEG has the advantage of being entirely silent and noninvasive. As we will see, MRI is quite noisy, and, of course, depth electrodes require surgery. Thus, MEG is attractive for use with children and vulnerable people. MEG is easy for young children to tolerate as long as they can stay relatively still.

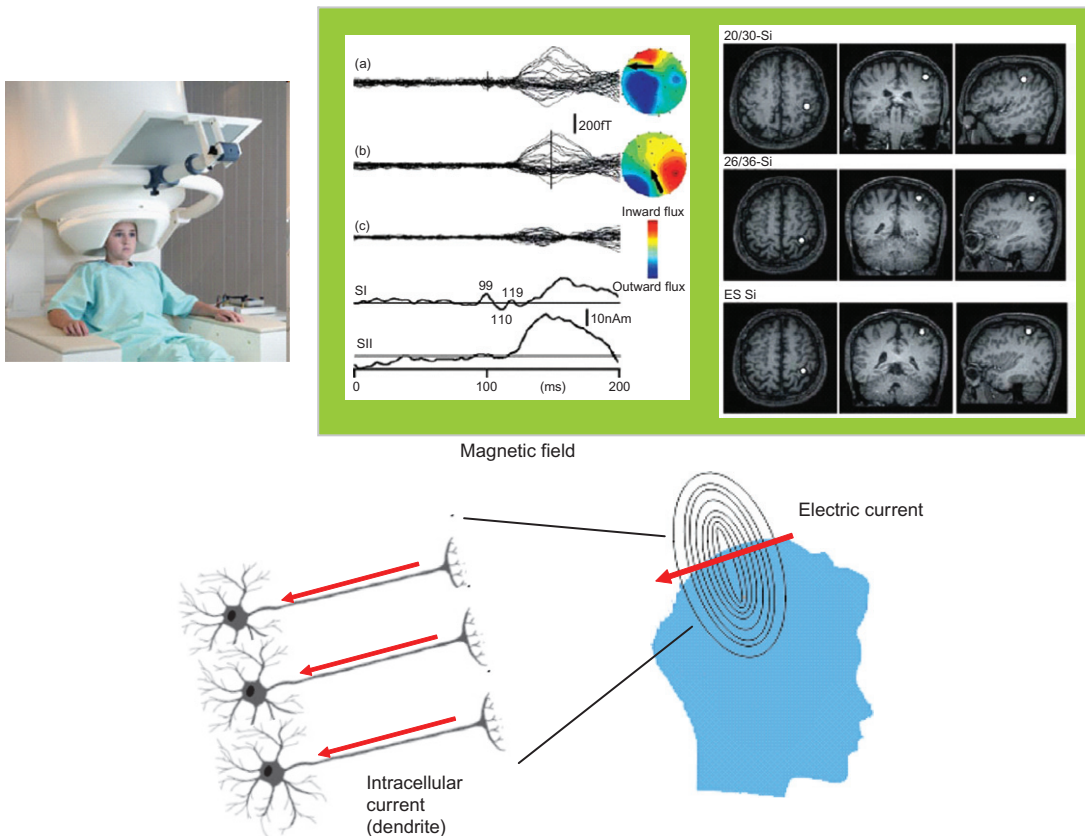


FIGURE 5.13 Magnetoencephalography and its analysis. The subject is placed in the scanner that has a large set of shielded sensors. The signals are derived from ionic currents flowing in the dendrites (bottom). Action potentials do not produce an observable field. Upper middle: Magnetic fields following painful (touch) stimulation, where (a) shows the recorded data, and (b) and (c) display residual magnetic fields obtained after filtering the somatosensory processing signals from the recorded data. The bottom two lines show the time course of the source strengths during the painful stimulation. Upper right: Source locations of the MEG data overlaid on MR images. Source: *VSM MedTech*.

3.0 FUNCTIONAL NEUROIMAGING: A BOLD NEW WORLD

EEG and MEG measure brain activity fairly directly. Other neuroimaging methods use indirect measures, such as blood flow or regional oxygen level. Currently, the most popular method is fMRI (Figure 5.14) and especially the kind that measures the oxygen level of the local blood circulation (called BOLD, for **blood-oxygen level dependent** activity).

When neurons fire, they consume oxygen and glucose and secrete metabolic waste products. An active brain region consumes its local blood oxygen supply, and as oxygen is consumed, we can see a small drop in the BOLD signal. In a fraction of a second, the loss of regional oxygen triggers a new influx of oxygen-rich blood to that region. Here, we see a recovery of the signal. However, as the compensatory mechanism overshoots, flooding more oxygenated blood into the area than is needed, we also see that the signal rises high above the baseline. Finally, as unused oxygen-rich blood flushes out of the region, we can see a drop in the BOLD signal back to the baseline (Figure 5.15).

Thus, as the oxygen content of blood produces changes, we can measure neural activation indirectly. The BOLD signal comes about six seconds after the onset of neuronal firing. The relationship between neural activation and the BOLD fMRI signal is shown in Figure 5.16. Note that these studies frequently use a block design, where a certain task is cycled on and off and the BOLD signal is measured across the ON and OFF blocks.

Positron emission tomography (PET) was developed much earlier than MRI or fMRI, and it provides a measure of metabolic brain activity (Figure 5.17). PET is used less often for research today because it is very expensive, requiring a cyclotron. It also requires subjects to be injected with a radioactive tracer. For nonmedical investigations, MRI and fMRI have



FIGURE 5.14 An MRI scanner. For both MRI and fMRI recording, the subject is lying down on the narrow bed that is then drawn into the core of the scanner. Source: *Sharma & Sharma, 2004*.

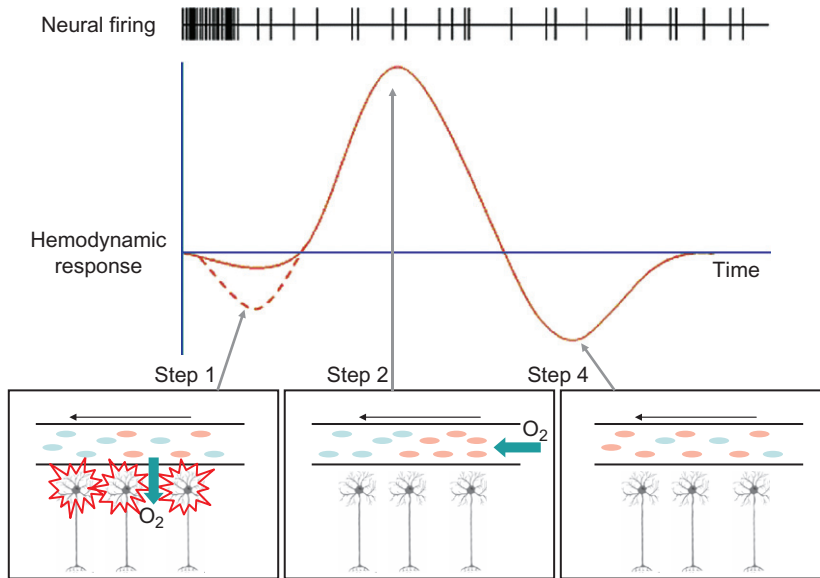


FIGURE 5.15 MRI and functional MRI. Top: The blood oxygenated-level dependent (BOLD) signal simplified in four steps. Step 1: increased neural activation leads to an increase in the consumption of oxygen from the blood, leading to a lower level of oxygenated blood and more deoxygenated blood, leading to a drop in the BOLD signal. Step 2: the vascular response to the increase in oxygen consumption leads to a dramatic increase in new, oxygenated blood at the same time as the oxygen consumption drops due to the decreased levels of neuronal activation. Step 3: a normalizing of flow and deoxy/oxyhemoglobin levels (not shown). Step 4: a poststimulus undershoot caused by the slow recovery of blood volume. Source: *Thomas Ramsoy, 2010, with permission.*

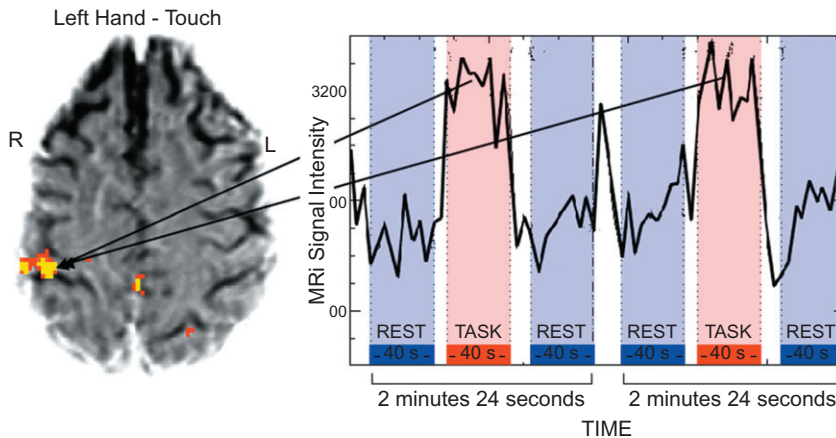


FIGURE 5.16 fMRI shows the activity of the brain, using a blocked design, where a stimulus is presented in blocks separated by a resting state, the BOLD signal cycles on and off as neural activity changes. Source: *Robinson, 2004.*

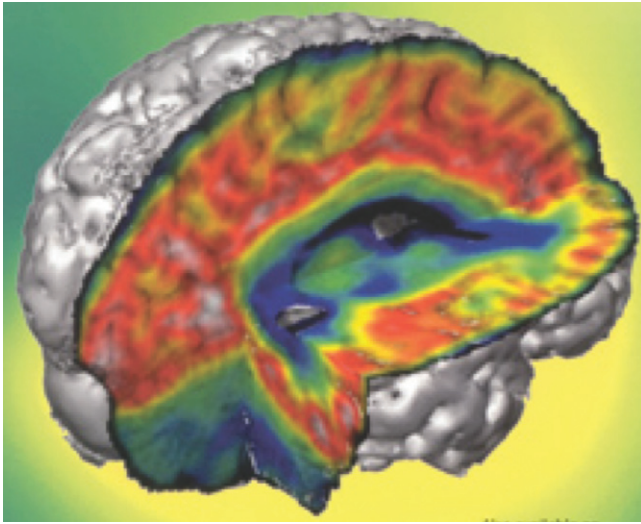


FIGURE 5.17 Positron emission tomography. PET measures metabolic activity in the brain. Here is an example of levels of metabolic activity across brain areas due to a certain neuroreceptor. The metabolic activity detected by PET has been coregistered with an MRI image that shows the brain anatomy. Source: *Adams et al., 2004.*

largely taken over the research field (Figure 5.18). However, PET is still important because different tracers can be linked to different molecules. The distribution of neurochemicals can therefore be determined.

Today, it is not possible to have high spatial and high temporal resolution at the same time using the same recording device. There is a tradeoff. Methods like fMRI and PET tell us *where* in the brain something is happening. EEG, MEG, and single cell recordings show millisecond changes in the brain. In any study, it is important to ask why the authors chose a particular method and what they observed—or might have missed—by the choices they made. In the best cases we can see different methods showing convergent results.

3.1 Regions of interest

Finding your way around the brain is not easy. An even harder task is figuring out which areas play which roles in major cognitive processes such as language, attention, and vision. One way is to define regions of interest (ROIs) ahead of the study and make predictions about expected activity in ROIs.

3.1.1 Coregistration of functional activity on a structural scan

The first step is to define the living brain anatomically to make out different areas, connections, and layers of organization. Structural MRI gives us a tool to map out brain structure, including the axonal (white matter) connections between brain regions. MRI shows structure but not function.

Look again at Figure 5.16, where the BOLD signal for a blocked fMRI design is presented. On the right side of Figure 5.16, we see an image with two yellow “hot spots,” reflecting increased fMRI activity. The color is arbitrarily chosen to indicate the degree of activity. In order to pin down the location of the yellow hot spots, we need to superimpose the functional image

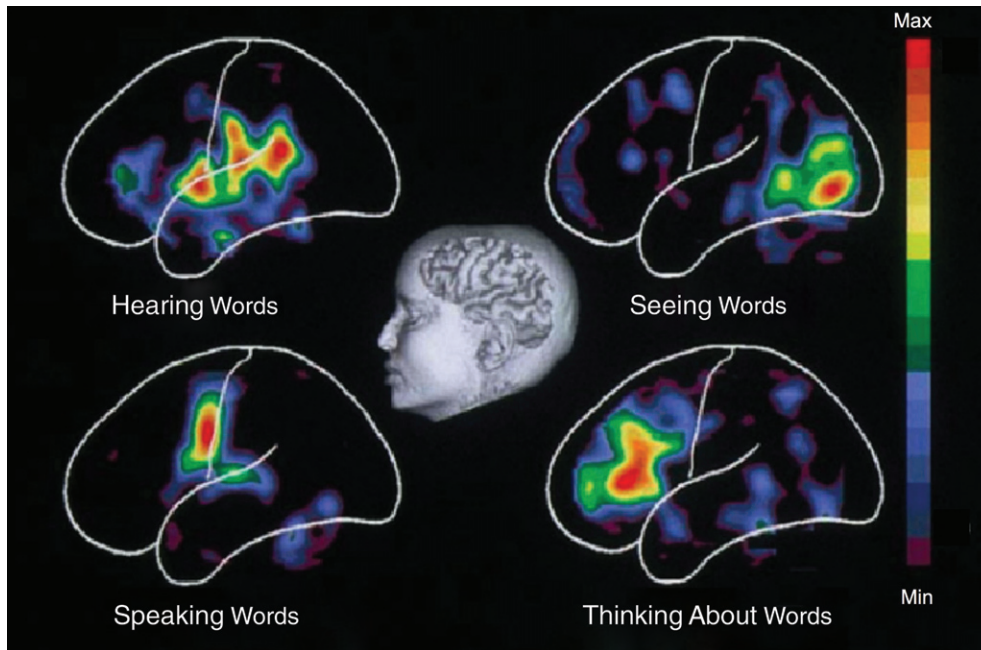


FIGURE 5.18 A classical PET finding: visual versus auditory brain activity. Brain metabolic activity is shown as noted on the right side of the figure, with red and yellow colors showing higher activity and blue and green colors showing lower activity. These early PET scans show results for hearing, seeing, speaking, and internally generating words. Notice that the auditory, visual, motoric, and speech production regions appear to be activated for the respective conditions. For example, in the “hearing words” condition, auditory regions in the temporal lobe show a high level of activity, while in the “seeing words” condition, visual regions in the occipital lobe show a high level of activity. Note that in these early studies, the results are shown on a brain outline template. Current studies use fMRI with enhanced ability to show brain function coregistered onto anatomical images. Source: *Posner & Raichle, 1997*.

on the structural MRI, which has a better spatial resolution. In a process called *coregistration*, the functional and structural images are aligned to each other. Coregistration ensures that the two images end up in the same space using the same metric. With higher spatial resolution we can ask questions that are anatomically specific.

Another approach is to mark ROI on the structural image alone to constrain the statistical analysis. Newer MRI machines with higher magnetic field strength now make it possible to look at the cellular organization of the living brain and to compare brains between groups of people (e.g., people with schizophrenia and healthy subjects).

3.1.2 Subtraction methods for defining functional activity differences

Different layers of cortex have either local or distant connectivity, so layer information is useful to find out how cortical regions interact. Because the brain is remarkably active at all times, it is still a challenge to isolate fleeting, task-related activity. One common method is

subtraction between fMRI conditions—for example, the brain’s response to the task of interpreting Arabic numerals (1, 2, 3, . . .) is compared to its response to the same numbers when they are spelled out (one, two, three, . . .). Subtraction is used because it tends to remove most of the “irrelevant” brain activity that would otherwise drown out the signal of interest. It is much like comparing a choppy sea before and after a whale swims by. If you want to see the waves generated by the whale alone, you might subtract a record of the waves alone. It is the *difference* between the two conditions that matters (Figure 5.19).

Subtracting conditions can have unwanted consequences. There might be important things going on in both conditions. In addition, the variance of experimental and comparison conditions might be different, there might be interactions between independent variables, and so

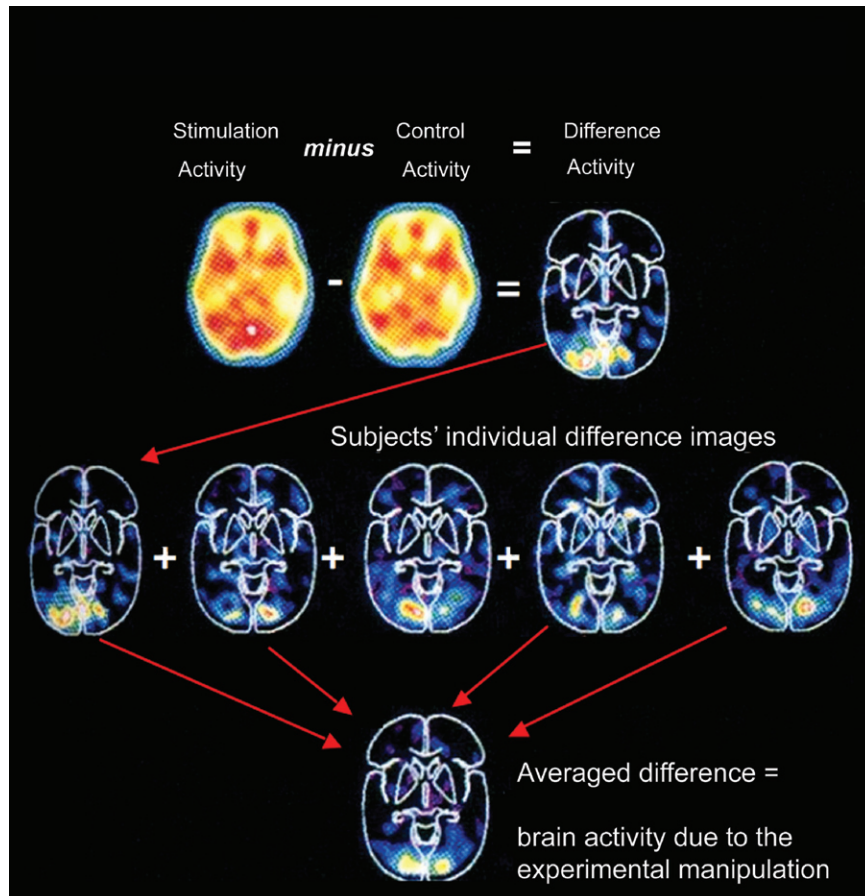


FIGURE 5.19 PET and fMRI subtraction methods. The brain has constant dynamic background activity. To remove this background activity, the PET or BOLD signal for an experimental task is subtracted, point by point, from a closely matched control task. Individual scans of the differences are then averaged and used to find the group average. Source: Posner & Raichle, 1997.

on. Another approach therefore is *parametric variation*, in which the variance for each main variable and their interactions can be separated statistically. For example, if you study working memory (WM), instead of subtracting brain activity during working memory from activity without it, one can study how gradually increasing the WM load leads to changes in neural activation. Since statistical testing must be done for every point of interest in the scan over every unit of time, this is a large data set.

3.2 The resting brain: intrinsic brain processes

As neuroimagers began to study different cognitive functions, the main approach was to use a contrastive, subtractive approach. Here, the neural activation during a given cognitive function, such as speech production, was compared to a period where subjects were instructed to relax and “do nothing.” Such active-versus-rest comparisons showed powerful effects.

Yet there is a hidden assumption in these studies. If you are asked just to lie still and “rest,” what will you do? Will your mind be a blank screen? A great deal of evidence shows that people just go back to their everyday thoughts, images, and feelings. You might be thinking about something that happened the day before or that you need to do later, or you might just daydream a bit. You are likely to have inner speech, visual imagery, episodic memories coming to mind, and so forth. For the brain, that is not “rest.” Instead, the experimental comparison is really between two active states of the brain. One is driven by experimental task demands, while the other reflects our own thoughts, hopes, feelings, images, inner speech, and the like. In some ways, spontaneous activity may tell us more about the natural conditions of human cognitive activity than specific experimental tasks. Both are important.

The use of MRI to produce both precise anatomical images and to provide functional maps of brain areas has revolutionized the field.

3.3 Structural changes in the brain: taxi drivers

The best science is done by combining imaging techniques with genuine creativity. A lot of creativity goes into the selection of functional variables. What is the best way to understand vision? To understand selective attention and conscious cognition? A great deal of ingenuity has been devoted to those questions. Let us consider a few examples. Taxi drivers are well known for their ability to know their way around a city. They know not only how to get from A to B, but they also know the most efficient way to get there. Such ability to navigate through a complex road system depends on our spatial ability. Studies have shown that the hippocampus, a part of the medial temporal lobe, plays an important part in the navigational memory of places and routes. Rats with lesions to the hippocampus have been known for decades to perform disastrously on spatial tests. Birds and other animals that bury or hide their food at multiple places have larger hippocampi than nonstoring animals. Therefore, one question that arises when we think about taxi drivers is, are the brain regions responsible for spatial navigation more developed in taxi drivers than in other people? Indeed, it has been found that part of the hippocampi of taxi drivers was larger than the same region in a group of people

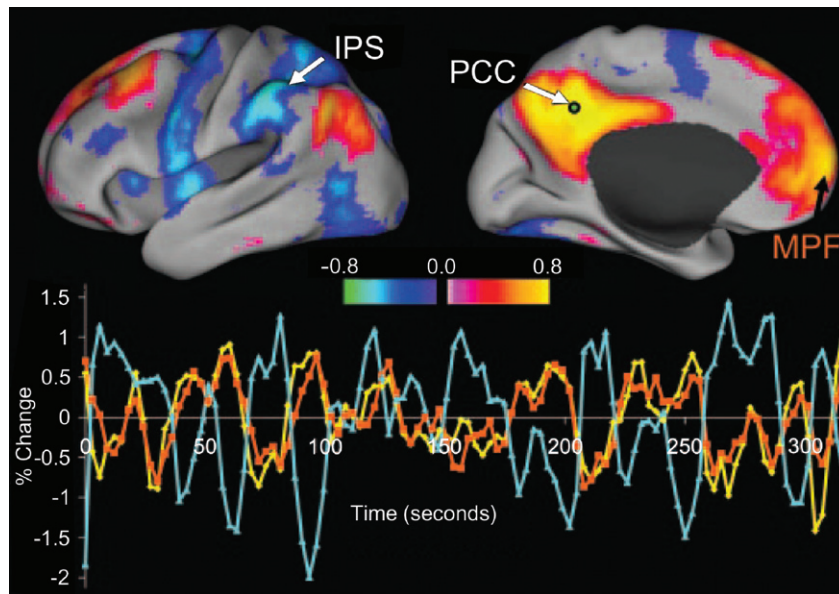


FIGURE 5.20 The brain is an active place. This fMRI shows spontaneous brain activity in both the left (shown as a lateral view on the left) and right (shown as a midline view on the right) hemispheres. The bottom shows this activation over 300 seconds (5 minutes). While such “task-unrelated” activity is different from typical experimental tasks, we know that humans are constantly thinking, imagining, feeling, anticipating, remembering, and talking to themselves without being given a specific task to do. Source: *Fox et al., 2005*.

with a different background. Okay, you might be thinking, but what if people with large hippocampi choose to be taxi drivers and not vice versa?

Here, the study showed that the size of the hippocampus depended on how long people had been working as taxi drivers. In other words, the longer you work as a taxi driver (and use your spatial navigation ability), the bigger your relevant part of the hippocampus will become.

Notice how imaginative the taxi driver example was. It is usually easier to randomly select human subjects (usually undergraduate students!) to stand for the entire human population. But the fact is that there are differences in age, particular abilities and talents, and other cognitive capacities among “average” subjects. One important implication is that the size of brain structures may change with specific experiences (Figure 5.21) (Maguire et al., 2000). That claim has now been supported for other brain regions as well. The taxi driver study is therefore an excellent example of creative selection of comparison conditions.

3.4 Connectivity and causality

White matter fiber tracts are the vast internal highway system of the cortex. We can visualize these fiber tracts using an MRI method called *diffusion tensor imaging* (DTI). DTI uses water flow along the axons surrounded by white myelin to measure the relative direction of white matter tracts (Figure 5.22). DTI helps us to understand brain connectivity patterns

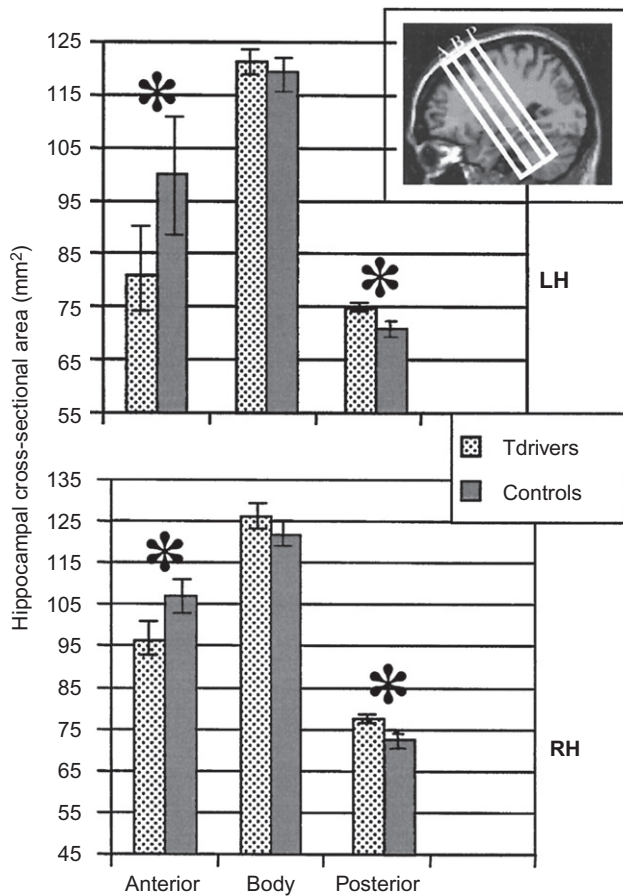


FIGURE 5.21 Memory and hippocampus size. Maguire and colleagues (2000) showed that London taxi drivers showed substantial differences in the size of a spatial mapping region of the brain, the posterior hippocampus. Source: Maguire *et al.*, 2000.

in the healthy brain, as well as investigate these patterns in individuals with brain diseases that affect white matter, such as multiple sclerosis.

By far the largest fiber bundle in the brain is the corpus callosum (see [Chapter 4](#)), which connects the two hemispheres; but there are many other fiber bundles or tracts that connect regions within the hemispheres. The view of the vast array of white matter tracts is shown in [Figure 5.23](#), with a midsagittal (center-line) view of the fiber tracts that extend upward from the spinal cord to the cortex. These fiber tracts make up the vertical “traffic arteries” that flow to and from the cortex and that provide the connective pathways throughout the central nervous system.

A recent study investigated the correspondence between white matter and gray matter, and the results are presented in [Figure 5.24](#). Constructed maps of peripheral white matter tracts are presented at the top of the figure, and their corresponding cortical gray matter regions are shown below. Note that [Figure 5.24](#) shows the same information across three views of the brain: from the front or anterior perspective (a and d), from the same or lateral perspective (b and e), and from the back or posterior perspective (c and f).

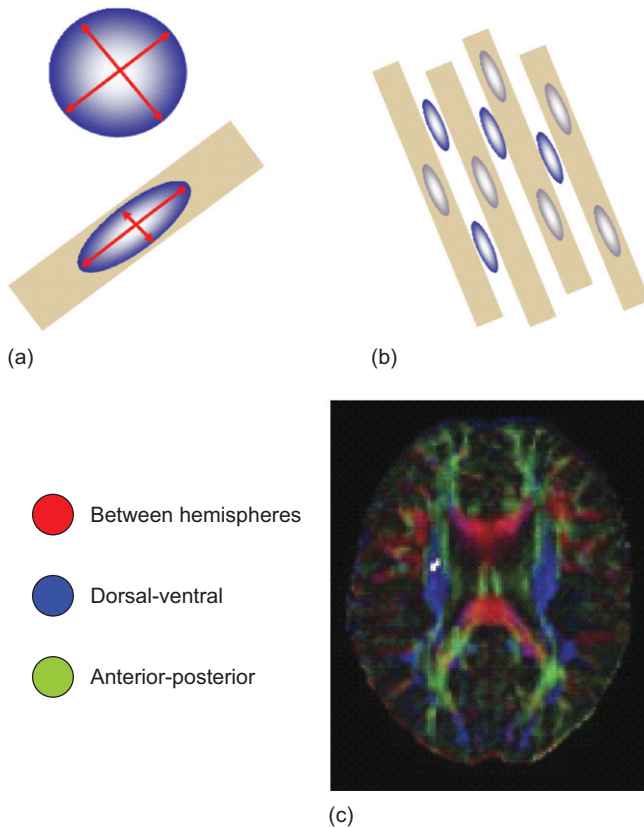


FIGURE 5.22 Diffusion of water depends on the local environment. (a) In the free and unrestricted medium (i.e., a glass of water), water can diffuse freely. The diffusion is *isotropic*—that is, it has the potential to move in all directions. If the water molecule is physically restricted, it can no longer move freely in any direction. This diffusion is *anisotropic*, meaning it cannot move in any direction. In a medium of fibers such as the brain’s white matter (schematically shown in (b)), water molecules are highly restricted by the axonal fibers. In this way, it is possible to visualize the fiber tracts of the brain and to estimate the integrity of white matter within a given region. (c) Such visualization produces the typical colored DTI brain image that displays different trajectory trends in regional white matter. Source: Thomas Ramsoy, 2010, with permission.

4.0 CORRELATION AND CAUSATION

We typically combine brain and behavioral observations. We can present visual images on a screen and have the subject read aloud or meditate. Thus we typically observe a *correlation* between behavior and brain activity. In methods with high spatial resolution, such as fMRI, different tasks show local increases or decreases in the BOLD signal, indicating that the brain works more in some regions than others (see [Figure 5.16](#)).

We can take the example of the Counting Stroop Task, in which subjects are asked simply to count the number of words shown on a screen. On some occasions a word like *dog* is shown three times. The subject should say “three,” which is not difficult. However, we can introduce a conflict between the words shown and the number of words. If we show the word *one* four times, there is an automatic tendency for expert readers (like college students) to say the word “one.” But the correct answer is “four.” This is very much like the Color-Naming Stroop Task. Subjects take longer to answer correctly, since they must inhibit their automatic tendency to read the words on the screen.

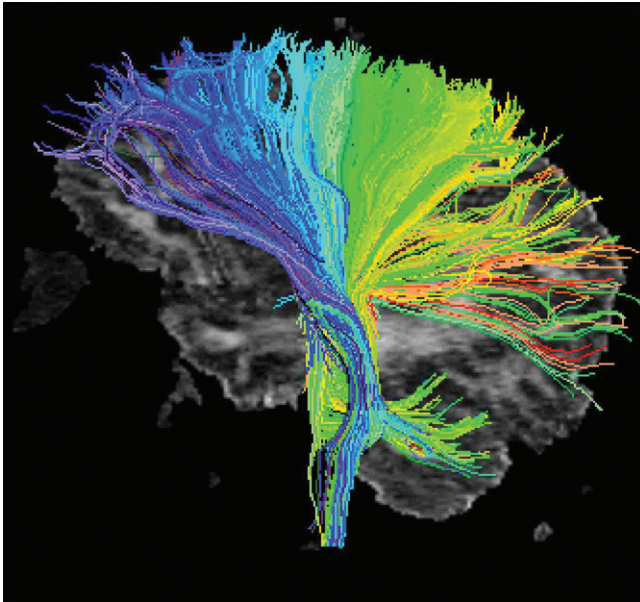


FIGURE 5.23 A fountain-like image of the white fiber tracts. This beautiful spray of neuronal tracts results from an MRI imaging technique called diffusion tensor imaging (DTI), which allows us to view the white (myelinated) fiber tracts. These are the vertical traffic arteries that flow from the cortex (especially frontal regions, shown in blue), down the spinal cord, and upward from the spinal cord to the rear half of the cortex, shown in yellow and green. Most of the volume of cortex is taken up by these massive fiber tracts. Source: Maria Lazar, with permission.

Zheng and Rajapakse (2006) reported the BOLD activity during the Stroop task (Figure 5.25). While many brain regions show activation during both conditions, frontal parts of the brain were more active during the conflict condition. This Stroop task result has now been found many times for conflictual tasks. One of the major roles of prefrontal cortex is to resolve conflicting tendencies, like the automatic tendency just to read words, against the tendency to follow the experimental instructions. Thus we have a correlation among (a) frontal activation, (b) longer reaction times, (c) a sense of subjective effort, and (d) a greater number of errors in the conflict condition. These are significant results, since there are many real-life conditions where conflicting tendencies need to be regulated.

However, so far we have no way to test *causal* hypotheses among the many brain regions that are involved in any complex task. For example, we know that the task requires visual word recognition, response preparation, choosing between two possible answers, perhaps detecting conflict, stopping the wrong answer from being said, selecting the right answer instead, and so on. An approach called *dynamic causal modeling* (DCM) is used to analyze causal relationships. Zheng and Rajapakse (2006) performed DCM on the brain activation they found in both word counting tasks. As you can see in Figure 5.25, DCM suggested that each task had a different activation pattern. Although many of the same regions of the brain are active during both tasks, their relative connectivity and contribution were altered. Interestingly, the analysis also showed that the interference condition recruits wider activity than the control condition. This is another common finding for mentally effortful conditions (Duncan & Owen, 2000).

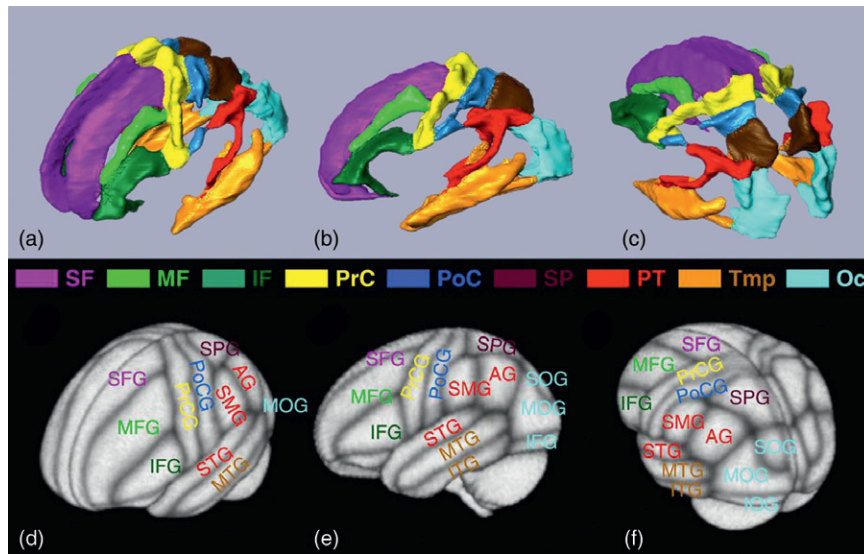


FIGURE 5.24 Diffusion tractography brings out the corpus callosum and other large fiber tracts. Notice that we are looking at a cutaway image of the brain, in which the right hemisphere is intact. We can see the green-marked fibers projecting upward in front and yellow-marked ones projecting toward the rear. Different artificial colors are assigned by computer to different directions of travel of the fiber highways (shown in (a), (b), and (c) – which are views of the same data, just shown in different angles. (a) shows the fiber tracts with a view from the front of the brain, (b) shows the same with a view taken from the side of the brain, and (c) shows same with a view from the rear of the brain). The c-shaped or banana-shaped structures in section (b) are the corpus callosum (the “calloused body”), which looks white to the naked eye. The corpus callosum contains about 100 million fibers, running sideways from one hemisphere to the other. Millions of cells in the left hemisphere connect to a corresponding point in the right hemisphere. Figures (d), (e), and (f) show the same views of the brain as those shown in (a), (b), and (c), in this case the entire brain surface is shown along with labels of these anatomical regions such as SFG - Superior Frontal Gyrus, and MFG - Middle Frontal Gyrus. Source: *Huang et al., 2005*.

4.1 Why we need multiple tests of brain function

According to some media headlines, brain scientists recently discovered the parts of the brain used for deception and lying. This kind of headline comes from studies like the one shown in [Figure 5.26](#). It shows fMRI differences between brain regions that had greater BOLD activity when people were telling the truth (green) and cortical areas when they were made to tell a lie. Such experiments often use playing cards and ask a group of subjects to “lie” by reporting a different card than the one they actually see.

One major purpose of cognitive neuroscience is identifying function with structure—that is, seeing whether specific brain locations do specific things for us. In that process, however, we must be very clear about the kinds of inferences that we can make from the evidence. The popular media may not be quite as careful as scientists need to be. Do you believe that the green areas in [Figure 5.26](#) are really the “truth-telling” areas of the brain?

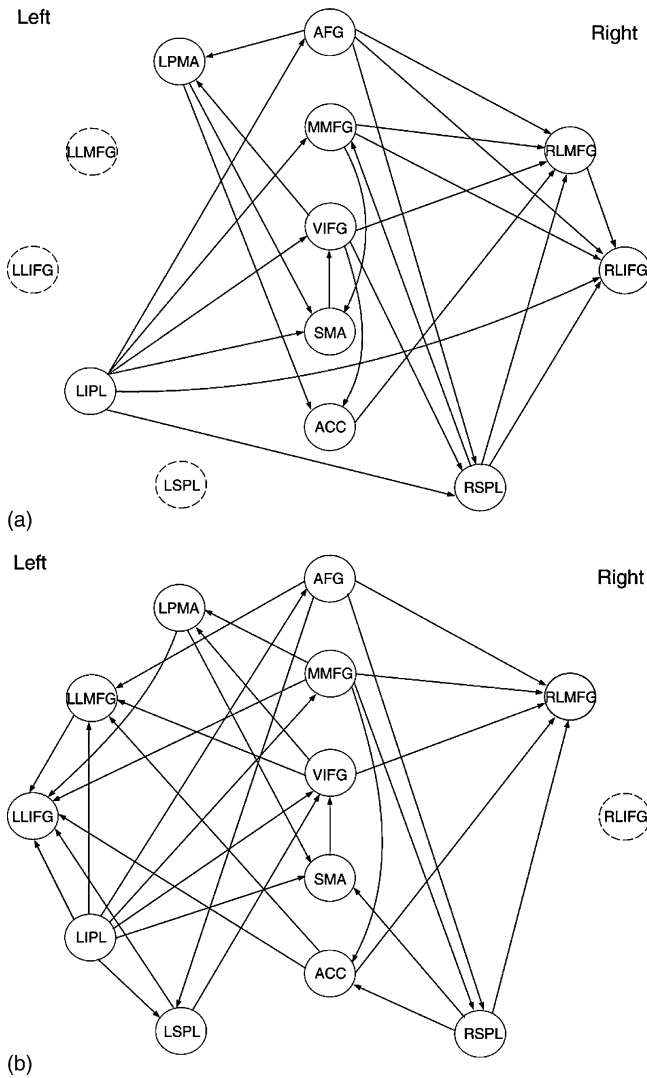


FIGURE 5.25 Causal relationships between brain activities during the Stroop task. Brain activity during simple counting with no interference is shown at the top (a), and the activation during counting with interference is shown at the bottom (b). Each circle represents a region of the brain. As can be seen, interference (b) leads to the engagement of a more widespread network than the control condition (a). This change in causal coupling between brain areas is seen in spite of the fact that many of the same areas are activated in both conditions. Note also that some of the connections are lost between the control (a) and interference (b) conditions. Source: Zheng & Rajapakse, 2006.

4.2 Brain damage and causal inferences

Historically, Paul Broca discovered patients who were unable to speak and also showed damage to the left frontal lobe. However, their ability to comprehend language was relatively spared. About the same time, Carl Wernicke made the discovery that damage to different regions of the left hemisphere was associated with the ability to understand language, while their ability to speak was intact. Today, we call this complementary pair of facts a *double dissociation*.

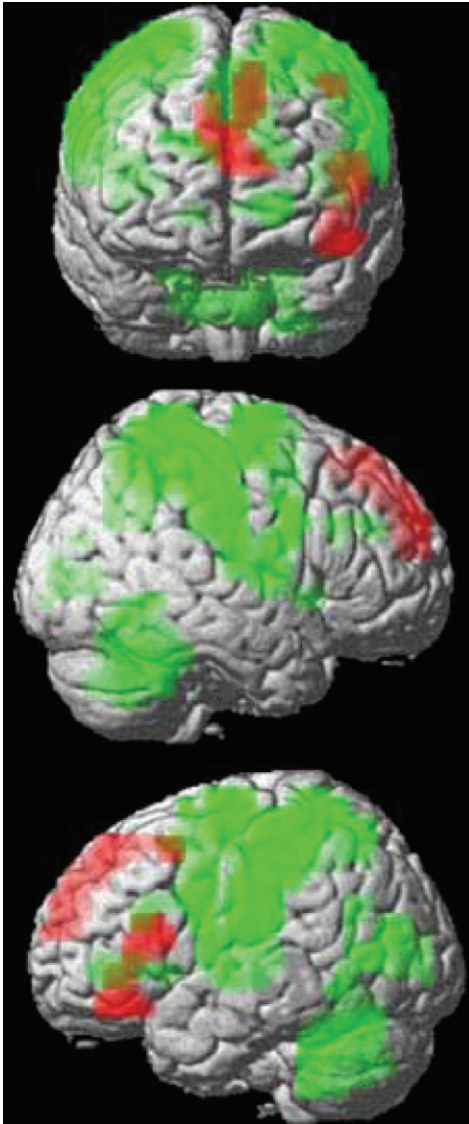


FIGURE 5.26 Are these the truthful and deceptive areas of the cortex? fMRI differences between cortical areas that had greater BOLD activity when people were telling the truth (green) and cortical areas when they were made to tell a lie (red). Is this the truth-telling cortex (green) and the lying cortex (red)? Why or why not? Source: *Davatzikos et al., 2005*.

Brain damage is correlational, since we cannot produce it and test its results in humans. Nevertheless, after a great deal of debate and controversy, there is no serious doubt today that one important function of Broca's area is the production of speech and likewise that one important function for Wernicke's region is speech comprehension ([Figure 5.27](#)). Lesions near Broca's area can lead to *dysarthria*, a condition where the control of mouth and tongue movement is disrupted but language production is still intact. Thus we have three lesions that lead to three different speech problems: one seems to be important for language

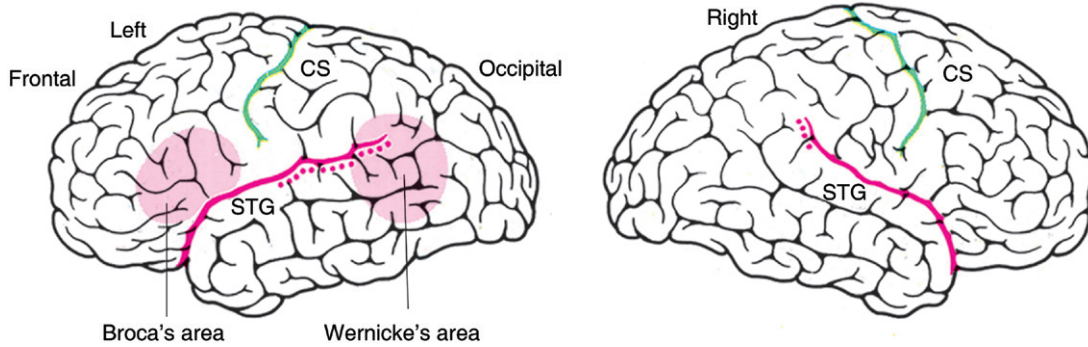


FIGURE 5.27 Language area lesions. Lesions to either Broca's or Wernicke's area produce very different effects on language. Abbreviations: CS = "central sulcus," STG = "superior temporal gyrus." Source: *Standring et al., 2005*.

comprehension; another is vital for language production; and a third region is important for the motor commands to produce vocal expressions.

Brain injuries in humans happen for a host of reasons, ranging from car accidents to strokes. Accidental lesions do not neatly follow the borders between brain regions. To test brain-mind hypotheses, it is preferable to be much more precise about exactly where in the brain deficits occur. In order to do this, studies have been conducted in experimental animals, typically rats and monkeys. However, language is a species-specific function for humans, and we have no direct parallels in other species. Safer brain interventions for the human brain are being explored, including TMS, electrical field stimulation, and even color lasers.

Very precise lesions have been studied in monkeys and rats for many years. For example, Buckley and Gaffan (2006) made precise lesions in different areas of the medial temporal lobe (MTL) in macaque monkeys. Very specific damage to the *perirhinal* cortex (meaning "near the smell cortex") caused monkeys to make more errors on a visual object discrimination task. Lesions to surrounding areas did not produce this deficit. The harder the discrimination task became, the more errors the lesioned monkeys made. Yet the monkeys performed normally in simple visual discriminations among different colors, shapes, and orientations. This suggests that the perirhinal cortex may have a specific *causal* role in processing complex visual objects, like faces. A variety of human studies now support this finding. Animal studies have often played this pioneering role, allowing us to pick up leads that are later tested in humans.

5.0 SUMMARY

Brain techniques measure single neurons to large cortical regions, brain structure, dynamic brain activity, and connectivity. The advent of brain imaging has transformed the study of human cognition. New and more refined methods are constantly being produced. One recent advance is using multiple methods in the same study to optimize the tradeoffs between direct and indirect measures of brain activity.

6.0 STUDY QUESTIONS AND DRAWING EXERCISES

1. Label the differences between the brain scans in [Figure 5.28](#), and describe the reasoning of the subtraction method for each image.
2. Define the BOLD response. What does BOLD stand for?
3. What is the time lag between neural activity and a BOLD response? Between neural activity and an EEG response?
4. What are the pros and cons of single cell recording in the brain?
5. What problem might arise when brain activity in a cognitive task is compared to a resting baseline?
6. What does [Figure 5.26](#) tell us about lying and the cortex?

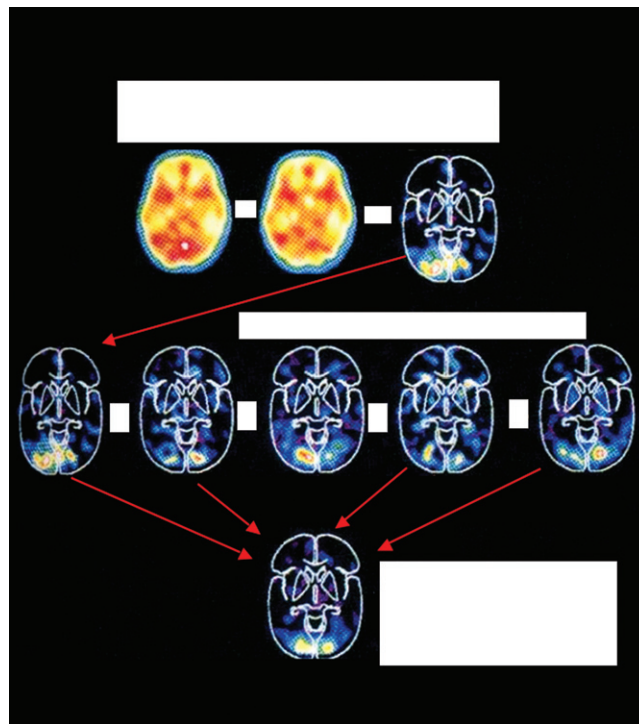


FIGURE 5.28 Drawing exercise. A reproduction of [Figure 5.19](#) shown without labels for use in the drawing exercises. Source: *Modified from Posner & Raichle, 1997, with permission.*

The art of seeing

OUTLINE

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THE MOVING SPIRAL

The question is not what you look at, but what you see. *Henry David Thoreau*



Stare at the center for ten seconds, and begin moving your eyes around the outer perimeter. Does it appear to be moving, shimmering, or just making you dizzy? Also, follow the outermost groove and watch it change from a groove to a hump as you go around the wheel.

Source: *Optical Illusions and Pictures*, <http://www.123opticalillusions.com/pages/opticalillusions14.php>, with permission.

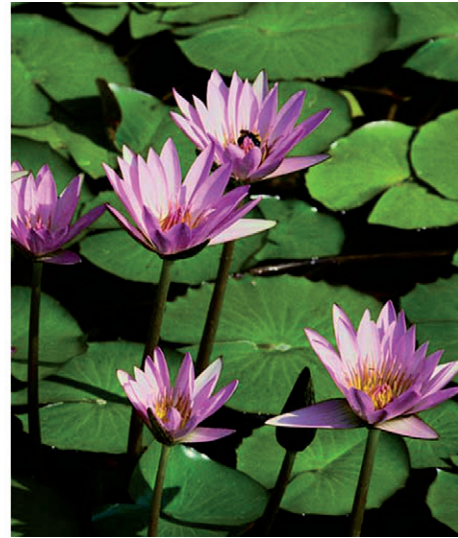
1.0 INTRODUCTION

1.1 The mystery of visual experience

Think back to the last time you stood atop a high lookout and gazed at the world below. Perhaps you were at the top of a summit and could see the wide expanse of the horizon cut by repeating mountaintops, forests, valleys, and rivers below, or perhaps you were at the top of a tall building as the bustling, swirling colors of rush-hour traffic, cars, and people flowed through the streets. It's worth pausing for a moment to think about how such vivid and powerful impressions can be the simple result of a collection of neurons firing inside your brain. How can the collective electrical activity of billions of neurons be responsible for everything you are seeing and experiencing at this very moment? These are some of the perplexing but fascinating questions that arise when we consider the relationship between brain activity and subjective visual experience.



(a)



(b)

FIGURE 6.1 Visual experiences. (a) Just one of millions of images you can experience with your visual system. Unlike the camera, you actually experience the image; you know what it is you are looking at. (Image courtesy of the Tong lab.) (b) Another example of the detailed, multifeature capabilities of your visual system. You can differentiate many different orientations, colors, and shapes. Source: *Frank Tong (2003), with permission.*

Most people intuitively think that human vision works much like a camera (Figure 6.1a). As we go about our daily activities, it is easy to believe that we see our entire world in crisp full-resolution color—much like a high-resolution photograph. However, as it turns out, this is far from the case. Due partly to the structure of our eyes, our visual perception is in full color and high resolution only at the center of gaze. This may seem hard to believe as you dart your eyes around the room now; the illusion that you are experiencing the whole visual scene in full color and clarity seems convincing. However, if you fix your gaze at a particular point in space—say, the corner of the windowsill or this word on the page—and get someone to hold up some fingers out at the edge of your field of view, you will find that without moving your eyes it is extremely hard to count the number of fingers he or she holds up. Also, you may notice that your experience of color is somehow dull and lacking in richness.

There are several reasons why it makes sense to restrict high-resolution vision to only a small portion of our visual space. This is just one of the many strategies that the brain uses to help represent the specific features and objects we see in the most efficient and effective way possible. It is a testament to the brain's ability seamlessly to represent the outside world that we normally remain oblivious to this striking fact.

1.2 The purpose of vision: knowing what is where

For most people, vision may be the most important of the five senses for getting around in everyday life and getting things done. What is the purpose of vision? David Marr, an early vision scientist and computer expert, made the deceptively simple comment that the goal of

vision is “*to know what is where.*” For example, if you are walking or driving to the university to find a class in a new building, it is important to know *where are the other cars and pedestrians, is the light red or green, which way is that car going, how fast is it approaching, do I turn at this street corner, is this the building I’m looking for?*

Considering the goal of vision, it becomes clear that visual perception is far more complicated than simply taking a picture with a digital camera. A digital camera can capture the image projected from the environment and store it in an array of pixels. However, the camera doesn’t really do anything with this image and doesn’t have any knowledge about what is stored in the image, such as what objects are in the photo or where they are. The easiest way to figure out what is in the picture is to have someone look at the picture and interpret it with his or her brain. Visual perception is what happens *after* the picture reaches the eyes. The image forms a pattern of activity on the array of receptors in the eye, and the detailed pattern is analyzed by the visual centers of the brain, thereby revealing what is where.

1.3 Knowing what: perceiving features, groups, and objects

How does the brain perceive what something is? Studies of human visual perception and neuroscience suggest that there are many levels of perception. At the most basic level, the human brain appears to process basic *visual features* such as *color, orientation, motion, texture, and stereoscopic depth*. For example, when looking at the picture of the flower in [Figure 6.1b](#), we may perceive that the center of the flower is yellow, the leaf just below is green, and the two stems are each at different angles. We are very good at perceiving small differences in orientation (1–2 degrees of angular tilt), subtle differences in color (e.g., the red of a rose or the red of a strawberry), and very faint traces of motion.

Most neurons in early visual areas of the brain are highly tuned to specific features. Some may fire very strongly to a line shown at a particular angle, to a particular color, or to a particular motion direction. These neurons respond to a very small region of the visual field (i.e., your current field of view), ranging from just a fraction of a degree to a few degrees of visual angle. If you hold your thumb at arm’s length, the width of your thumb is probably about 2 degrees of visual angle (O’Shea, 1991).

If the activity of each of these neurons represents only a small part of the visual field, such as whether a small patch of the visual field contains vertical or horizontal, red or blue, motion or something stationary, then how is the brain able to combine this information across many neurons? Somehow, the brain is able to organize these basic feature elements into organized *perceptual groups*. The *Gestalt* psychologists proposed that perception could not be understood by simply studying the basic elements of perception (Wertheimer, 1912; Koffka, 1935). The German word *Gestalt* is difficult to translate directly, but it expresses the idea that *the whole is greater than the sum of the parts*. These psychologists proposed the *Gestalt laws of perceptual grouping*, such as the laws of *similarity, proximity, good continuation, common fate*, and so forth ([Figure 6.2](#)). These laws suggest that elements that are more similar in color or shape are more likely to be perceived as a group. Likewise, if a set of elements is arranged in a way that they are more closely spaced in rows or columns, this will determine whether they are perceived as rows or columns.

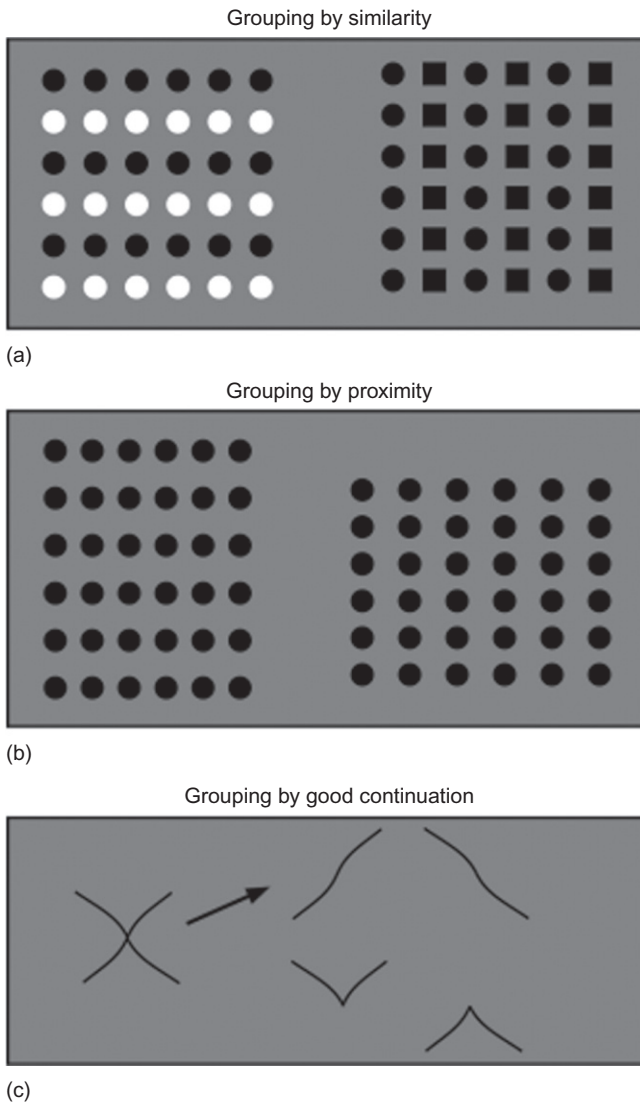


FIGURE 6.2 Gestalt grouping. (a) Grouping by similarity, the white dots are grouped with other white dots. On the right, the squares group with squares. The objects with similar features tend to group together. (b) Here, even though all the objects are circles, due to their grouped locations or proximity to one another, we perceive two separate groups of dots. (c) Grouping by good continuation. On the left, we perceive one object. On the right, the exact same lines are drawn but separated so that there is no continuation across the entire object. In all these cases, the collections of objects form groups or larger global objects, which are greater than the simple sum of the parts. Source: Frank Tong, with permission.

Why is perceptual grouping so important? It helps us perceive which features belong to a possible object, and it helps us to distinguish an object from the background. For example, imagine seeing a golden retriever lying in tall grass. Grouping by similarity may help us see that the dog is separate from the grass, and the neighboring wagging tail might be recognized as part of the dog, even though only the end of the tail can be seen.

Finally, we can perceive the shape of entire *objects* and match these shape representations to the objects we know from previous experience. To perceive an object, the brain has to go through many stages of visual processing, from processing the feature elements of the object,

putting the elements together into coherent groups, and finally figuring out how those elements form a coherent organized shape. This representation of the object's shape must then be matched to the correct object representation stored in memory. Given that there are thousands of objects and that the 2D image of any object projected onto the back of the eye can vary from changes in viewpoint, lighting, or viewing conditions, this makes the problem of object recognition especially challenging. Somehow, the brain must abstract the stable or invariant properties of an object while disregarding all the superficial ways in which the 2D image of an object can vary.

1.4 Knowing where things are

How do we know where objects are located in the world? When we look at the world, the image that strikes the back of our eye is essentially 2D, similar to the image that would be taken by a camera. This 2D map of the world projected onto the eye is preserved in the early visual areas of the cerebral cortex, which provides a map of where objects are located relative to the center of gaze. The brain is also able to figure out the missing third dimension and estimate how far away objects are in space. Whereas early visual areas represent the positions of objects relative to the center of gaze, higher brain areas in the parietal, temporal, or frontal lobe are more likely to represent the position of objects in a more abstract (less visual) manner, relative to the person's body position or relative to the global environment.

2.0 FUNCTIONAL ORGANIZATION OF THE VISUAL SYSTEM

When the light coming from an object reaches our eyes, it triggers a cascade of neural events as this visual pattern is converted into neural impulses that travel up the visual system from one brain area to the next. Through a series of neural processes in many brain areas, the activity of neurons in numerous brain areas somehow leads to the visual experience and recognition of the object and its many component features. Let's trace the sequence of events to understand how the brain processes visual information at each stage of visual processing. This will help us understand how different visual areas of the brain contribute to visual perception.

2.1 The retina

There are two types of photoreceptors in the retina: *cones* and *rods* (Figure 6.3). Cones are color-selective, less sensitive to dim light than rods, and important for detailed color vision in daylight. Each cone contains one of three kinds of *photopigments*, specialized proteins that are sensitive to different wavelengths of light. These wavelengths roughly correspond to our ability to distinguish red, green, and blue. When light strikes a photopigment molecule, the light energy is absorbed and the molecule then changes shape in a way that modifies the flow of electrical current in that photoreceptor neuron. Cones are densely packed into the *fovea*, the central part of the retina that we use to look directly at objects to perceive their fine details.

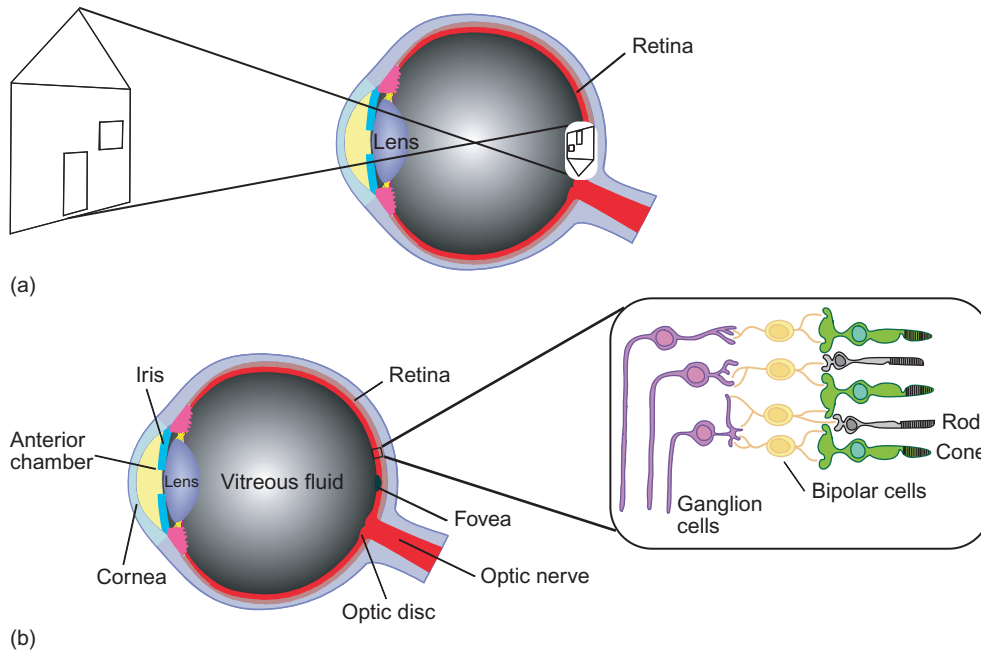


FIGURE 6.3 The eye. (a) Illustration showing how objects in the environment are physically projected to the back of the eye—the retina. (b) The eye and a cross-section of the retina. The cross-section of the eye shows where the photoreceptors are located in the retina. Both the rods and cones are shown. They respond to different types of light. The neural signal then travels via bipolar cells and then to the ganglion cells. The axons of the ganglion cells take the neural information out of the eye and backward toward the cortex. Source: Squire et al., 2008.

In the periphery, cones are more spread out and scattered, which is why objects in the periphery appear blurrier and their colors are less vivid.

Rods contain a different photopigment that is much more sensitive to low levels of light. Rods are important for *night vision*. We rely on seeing with our rods once our eyes have adapted to the darkness (*dark adaptation*). Curiously, there are no rods in the fovea, only cones, and the proportion of rods increases in the periphery. This is why you may have noticed when gazing at the night sky that a very faint star may be easier to see if you look slightly off to one side.

The signals from photoreceptors are processed by a collection of intermediary neurons, *bipolar cells*, *horizontal cells*, and *amacrine cells*, before they reach the *ganglion cells*, the final processing stage in the retina before signals leave the eye. The actual cell bodies of ganglion cells are located in the retina, but these cells have long axons that leave the retina at the *blind spot* and form the *optic nerve*. Each ganglion cell receives excitatory inputs from a collection of rods and cones; this distillation of information forms a *receptive field*. Ganglion cells at the fovea receive information from only a small number of cones, while ganglion cells in the periphery receive inputs from many rods (sometimes thousands). With so many rods providing converging input to a single ganglion cell, if any one of these rods is activated by photons of light, this may activate the cell, which increases the likelihood of being able to detect dim, scattered

light. However, this increase in sensitivity to dim light is achieved at the cost of poorer resolution; rods provide more sensitivity but also a “blurrier” picture than the sharp daytime image provided by cone vision.

Retinal ganglion cells receive both excitatory and inhibitory inputs from bipolar neurons, and the spatial pattern of these inputs determines the cell’s *receptive field* (Figure 6.4a). A neuron’s receptive field refers to the portion of the visual field that can activate or strongly inhibit the response of that cell. Retinal ganglion neurons have center-surround receptive fields. For example, a cell with an *on-center off-surround* receptive field will respond strongly if a spot of light is presented at the center of the receptive field. As that spot of light is enlarged, responses will increase up to the point where light begins to spread beyond the boundaries of the on-center region. After that, the response of the ganglion cell starts to decline as the spot of light gets bigger and stimulates more and more of the surrounding off-region. (A cell with an off-center on-surround receptive field will respond best to a dark spot presented in the center of the receptive field.)

How can the behavior of retinal ganglion cells be understood? A key concept is that of *lateral inhibition* (Kuffler, 1953). Lateral inhibition means that the activity of a neuron may be inhibited by inputs coming from neurons that respond to neighboring regions of the visual field. For example, the retinal ganglion cell in Figure 6.4b receives excitatory inputs from cells corresponding to the on-center region and inhibitory inputs from the off-center region. The strengths of these excitatory and inhibitory inputs are usually balanced,

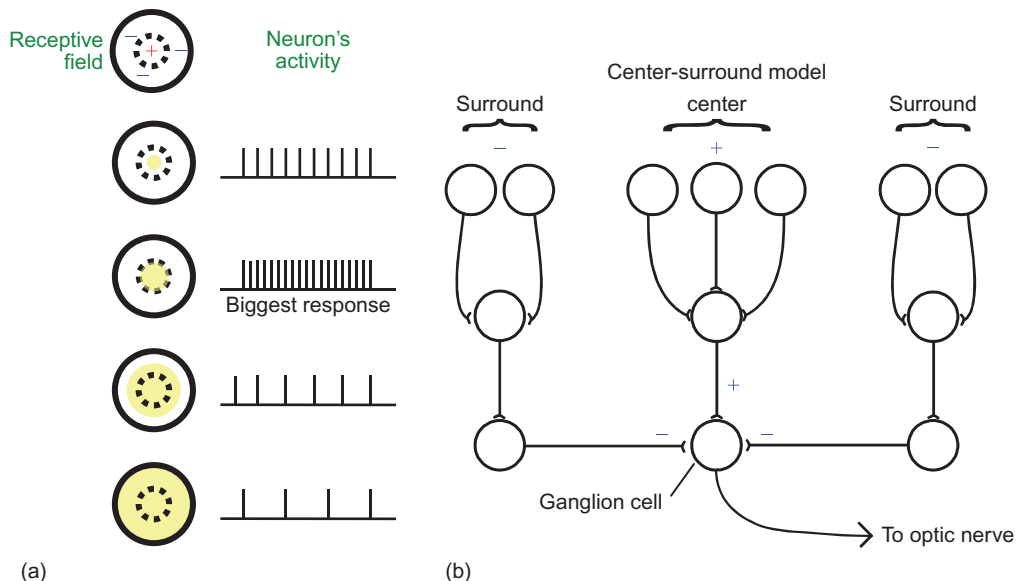


FIGURE 6.4 Center-surround receptive fields. (a) Schematic example of a center-surround cell’s response to different-sized patches of light. Notice that the biggest spiking response (shown by the lines on the right) occurs for the intermediate-sized center light patch. The spot of light has to be just the right size to get the maximum response out of that particular neuron. (b) A model of how a center-surround receptive field might be achieved by the collaboration and competition between different connective neurons in the retina. Source: Frank Tong, with permission.

so if uniform light is presented across both on- and off-regions, the neuron will not respond to uniform illumination.

Lateral inhibition is important for enhancing the neural representation of *edges*, regions of an image where the light intensity sharply changes. These sudden changes indicate the presence of possible contours, features, shapes, or objects in any visual scene, whereas uniform parts of a picture are not particularly informative or interesting. Figure 6.5 shows a picture of the fox in original form and after using a computer to filter out just the edges (right picture) so the regions in black show where ganglion cells would respond most strongly to the image. Lateral inhibition also leads to more efficient neural representation because only the neurons corresponding to the edge of a stimulus will fire strongly; other neurons with receptive fields that lie in a uniform region do not. Because the firing of neurons takes a lot of *metabolic energy*, this is much more efficient. This is an example of *efficient neural coding*; only a small number of neurons need to be active at any time to represent a particular visual stimulus.

Lateral inhibition also helps to ensure that the brain responds in a similar way to an object or a visual scene on a cloudy day and on a sunny day. Changes in the absolute level of brightness won't affect the pattern of activity on the retina very much at all; it is the relative brightness of objects that matters most. An example of this is if you see a friend wearing a red shirt. The *absolute level of brightness* of that shirt when you see your friend outside your house on a sunny day versus inside your house in a sheltered room will differ, but this will not affect the pattern of activity on the retina. On the other hand, the *relative brightness* of the shirt compared to other nearby objects or the background scene will make a difference on the retinal activity. Finally, lateral inhibition at multiple levels of visual processing, including the retina, lateral geniculate nucleus and visual cortex, may lead to interesting visual illusions such as the Hermann grid illusion (Figure 6.6).

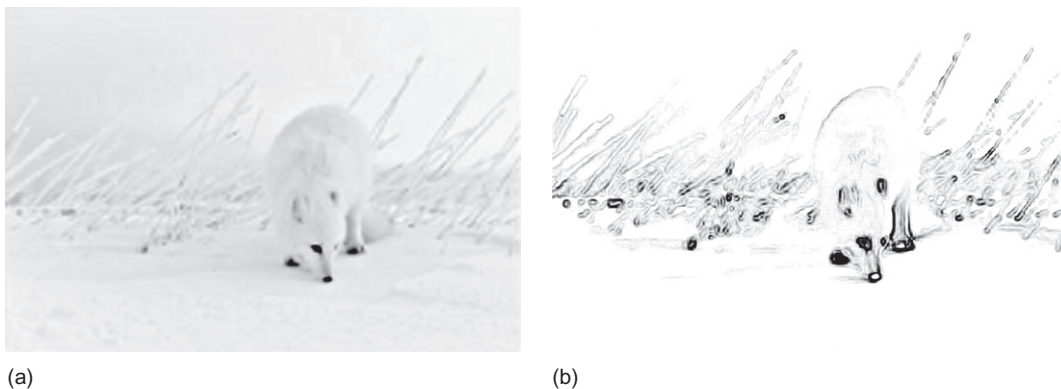


FIGURE 6.5 The edges hold the most information. An example of how most of the information in the picture comes from the edges of objects. (a) On the left is the original. (b) On the right is information from the edges only—taken from the image using a computer algorithm. Source: Frank Tong, with permission.

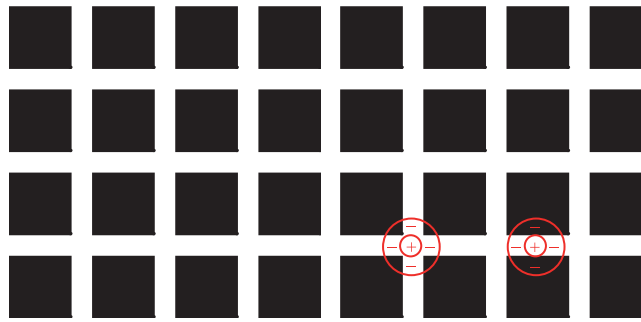


FIGURE 6.6 Hermann grid illusion. Take a careful look at the collection of black squares in the figure. Do you notice anything unusual? Do you have the impression of seeing small, dark circles in between the black squares in the periphery? Don't be alarmed; this is completely normal. This is a great example of receptive fields with lateral inhibition at work (Hermann, 1870). In the rightmost matrix of squares, some possible receptive fields are shown. A receptive field that falls between the corners of four dark squares will have more of its inhibitory surround (see [Figure 6.4](#)) stimulated by the white parts of the grid than a receptive field that lies between just two of the dark squares. As a result, neurons with receptive fields positioned between four dark squares will fire more weakly, leading to the impression of small, dark patches at these cross points. At the fovea, receptive fields are much smaller, so the illusion is only seen in the periphery. Source: *Frank Tong, with permission.*

2.2 Lateral geniculate nucleus

From the eye, retinal ganglion cells send their axons to a structure in the thalamus called the *lateral geniculate nucleus* (LGN). Specifically, the left half of each retina projects to the left LGN; the right half of the retina projects to the right LGN. For this to happen, the inputs from the nasal portion of each retina must cross at the *optic chiasm* to project to the opposite LGN ([Figure 6.7](#)). The result is that the left LGN receives input from the right visual field, and the right LGN receives input from the left visual field, so each LGN serves to represent the *contralateral* (i.e., opposite) visual field. Note that the inputs from each eye go to separate monocular layers of the LGN, so signals from the two eyes remain separate until they reach the *primary visual cortex*, where these signals are combined.

Receptive fields in the LGN share the same shape and basic properties of the retinal ganglion cells with center-surround receptive fields. The thalamus is often considered a way station for signals finally to reach the cerebral cortex, where the neurons start to respond in very different ways.

2.3 Primary—or striate—visual cortex

From the LGN, neurons send their signals to the primary visual cortex, sometimes called V1 because this region is the first cortical visual area. V1 is frequently referred to as “*striate*” cortex because of its distinguishing striped—or striate—appearance. About 90 percent of the outputs from the retina project first to the LGN and then onward to V1. The left LGN projects to V1 in the left hemisphere; the right LGN projects to right V1 (see [Figure 6.7](#)). In V1, the spatial layout of inputs from the retina is still preserved. Left V1 receives an orderly set of inputs from the left half of both retinas via the thalamus. The foveal part of the visual field

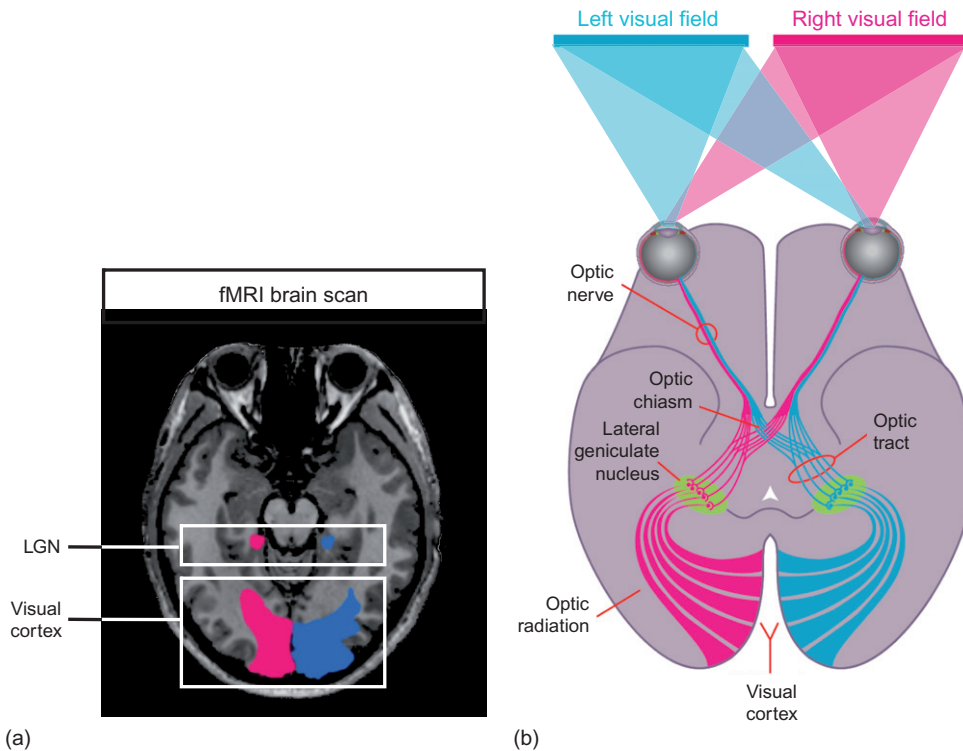


FIGURE 6.7 The visual pathways from retina to cortex. (a) Example of a brain slice from a functional magnetic resonance imaging (fMRI) scan, showing the lateral geniculate nucleus (LGN) and primary visual areas at the back of the brain (the occipital cortex). The two different colors denote the two hemispheres of the brain. (b) Schematic illustration showing the visual pathways from the retina in the eyes to the primary visual cortex at the back of the brain. You can see here that the neural information from the nasal or inner sides of the eyes crosses over at the optic chiasm to be processed in the contralateral side of the brain. The left visual field, in blue, is processed by the right visual cortex (also blue). The LGN, displayed in green, relays the visual information to the primary visual areas of the cortex. Source: *Squire et al., 2003*.

is represented in the posterior part of the occipital lobe near the occipital pole, and the more peripheral parts of the visual field are represented more anteriorly. Left V1 therefore contains a *retinotopic map* of the entire right visual field, while right V1 contains a map of the entire left visual field. This retinotopic organization is very prevalent in early visual areas (V1 through V4), where neurons have small receptive fields, but it becomes weaker and less orderly in higher visual areas outside of the occipital lobe.

Neurons in V1 are sensitive to a whole host of visual features not seen in the LGN. One of the most important visual features is *orientation* (Hubel & Wiesel, 1962, 1968). Some V1 neurons respond best to vertical lines, some to 20-degree tilted lines, and still others to horizontal lines and so forth. [Figure 6.8](#) shows an example of a model for V1 orientation selectivity. If a V1 neuron receives excitatory input from three LGN neurons with aligned center-surround receptive fields, then the V1 neuron will respond best to a matching oriented line. For example, if a vertical bar is presented, the neuron shown in the figure will respond at its strongest

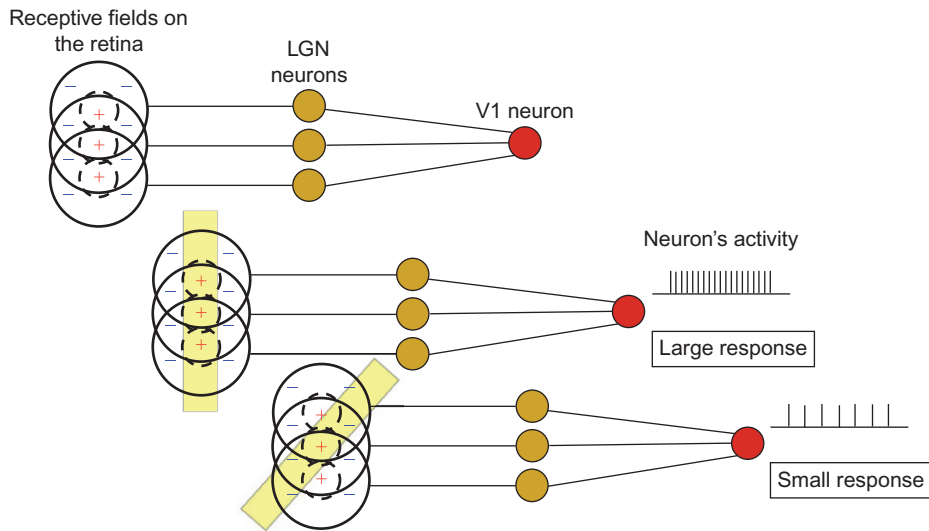


FIGURE 6.8 Orientation selectivity in V1. An example of how a collection of center-surround receptive fields could lead to orientation selectivity in V1 neurons. The overlapping circles on the left show center-surround receptive fields. When the bar of light lies vertically, it triggers all the on-centers of each receptive field, whereas when its orientation changes (the bar tilts), fewer centers and more surrounds are activated resulting in a smaller neural response (fewer spike bars in the graph). Hence the vertical bar gives a larger neural response, and when the stimulus is oriented, the magnitude of the V1 response is reduced. This constitutes orientation selectivity—only observed in the cortex. Source: Frank Tong, with permission.

because the entire excitatory region will be stimulated, whereas the inhibitory surround will not be stimulated. If the bar is tilted somewhat away from vertical, the neuron will respond more weakly because part of the inhibitory surround will now be stimulated and part of the excitatory center will not. Finally, if a horizontal bar is presented, the neuron may not fire at all because equal proportions of the center and the surround regions will be receiving stimulation, leading to a balance in the strength of incoming excitatory and inhibitory inputs. This configuration of center-surround receptive fields can explain the orientation selectivity of V1 neurons.

V1 neurons are also sensitive to many other *visual features* besides orientation (Hubel & Wiesel, 1998). Some neurons respond best to a particular *direction of motion*, such as upward motion, leftward motion, or downward motion. Other neurons respond best to particular colors or color differences (e.g., red versus green, yellow versus blue), though some basic types of color-sensitive neurons can also be found in the retina and LGN. Finally, some neurons respond best to particular *binocular disparities* (Barlow et al., 1967; Cumming, 2002), which refer to the degree of alignment between images in the two eyes. Small displacements between images in the two eyes are what allow us to perceive stereo-depth when we look at objects with both eyes open. (Close one eye, extend your arms to full length, and try to quickly bring your two index fingers to meet each other. Now try this again with both eyes open. If you have normal binocular vision, this should be much easier to do with both eyes open because you can better judge the distance of your two fingers.)

So how will V1 neurons respond to the outline of the house shown in [Figure 6.9](#)? A V1 neuron that is tuned to 45-degree tilted lines and has its receptive field in the position along the roof may fire strongly to the angled roof. A V1 neuron that responds best to vertical will help signal the presence of the vertical wall and a horizontal neuron will respond to the ceiling or floor of the house. In this sense, it can be readily seen that V1 neurons do much more than respond to simple spots of light, as the LGN does. V1 neurons provide a *neural representation* of the orientation of visual features that comprise the contours and shapes of objects. [Figure 6.9](#) provides a summary of the hierarchy of visual processing. From the LGN, V1, V4 to the ventral temporal cortex, you can see that neurons gradually respond to more complex stimuli from one area to the next.

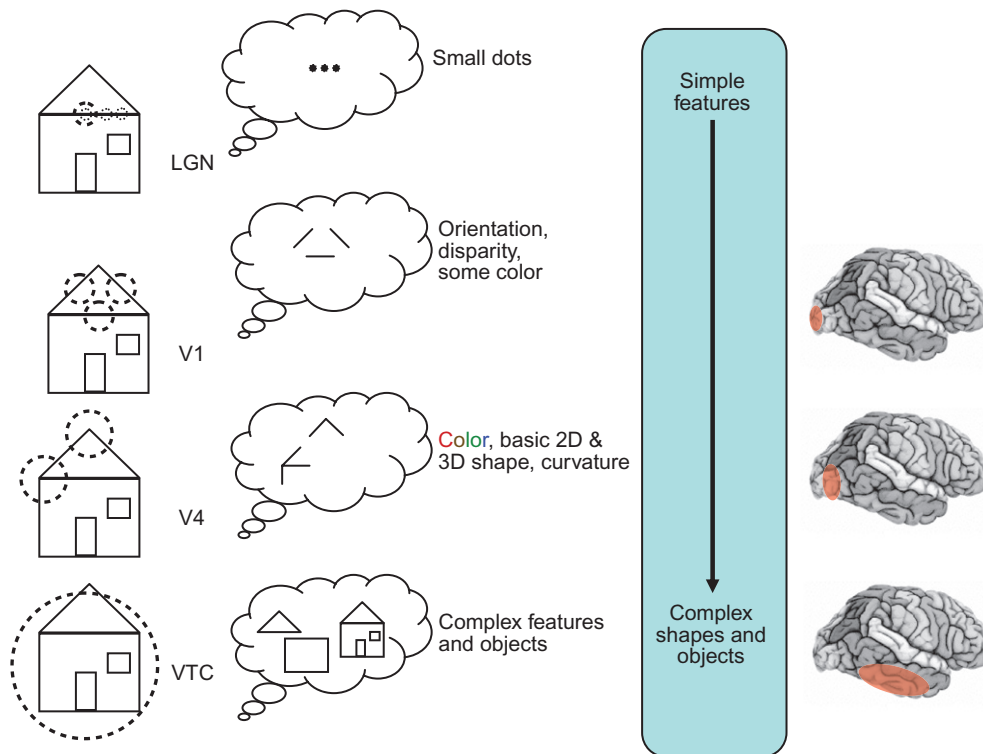


FIGURE 6.9 The hierarchy of visual processing. A demonstration of the hierarchical response properties of the visual system to simple and complex stimuli. The leftmost column shows a figure of a house which contains simple shapes—such as the triangle of the roof and the rectangles of the door and windows—along with other more complex features which together form a percept of a ‘house’. The receptive fields that would respond to this house image are shown with the dotted lined circles, beginning with neurons in the LGN which would respond to simple features such as the small dots in a printed line, moving on to neurons in V1 which would respond to the orientation of the lines forming the roof, and continuing on to neurons in the VTC, which would respond to the complex image itself. The rightmost column shows an estimate of where each area is in the brain. You can see that early visual areas respond to simple features and, as we move along the processing stream, areas respond to more complex shapes and objects. This is a well-established theme of the visual system. Source: *Frank Tong, with permission.*

So, to summarize, V1 is important in analyzing the visual features at a fine level of detail. These neurons have small receptive fields that are sensitive to orientation, color, motion, or binocular disparity. After visual signals are analyzed in V1, they are sent to higher visual areas for further processing.

2.4 Extrastriate visual areas—outside of V1

V1 sends *feedforward* signals to many higher visual areas, including areas such as V2, V3, V4, and *motion-sensitive area MT*, to name a few (Figure 6.10) (Felleman & Van Essen, 1991). Area V4 is known to be especially important for the *perception of color* (Zeki, 1977), and some neurons in this area respond well to more complex features or combinations of features

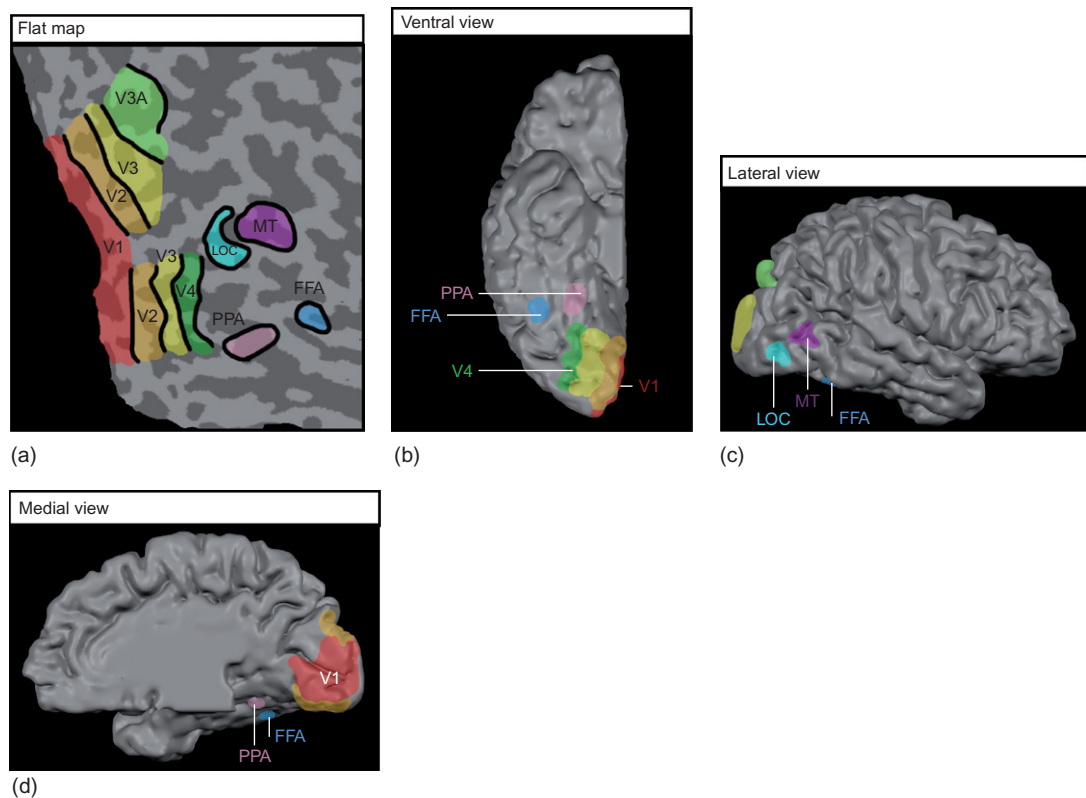


FIGURE 6.10 Visual areas of the brain. Functionally defined visual areas of the human brain, shown on a reconstruction from anatomical brain scans. (a) A flattened cortical representation of the human visual system. The flat map was created by unfolding the convoluted surface of the cerebral cortex, applying a cut through the calcarine sulcus, which divides area V1 into dorsal and ventral halves, and flattening the cortical sheet using computerized methods. This allows one to see all the visual areas of one hemisphere, including those buried in the sulci, in a single image. The upper half shows dorsal portions of visual areas V1, V2, and V3, as well as V3A. The lower half shows ventral visual areas V1, V2, V3, and V4, as well as the parahippocampal place area (PPA) and fusiform face area (FFA). Areas LOC and MT are also shown. (b) A ventral view of one hemisphere, showing the location of these areas in the cortex. (c) Lateral view of the same hemisphere, showing the positions of the different visual areas. (d) A medial view of the hemisphere showing mainly V1. Source: *Squire et al., 2003*.

(Pasupathy & Connor, 2002). For example, some V4 neurons are sensitive to curvature or to two lines that meet at a specific angle. These neurons might signal the presence of a curving contour or a corner. From our example of the house, a V4 neuron might respond best to the meeting of the two lines forming the point of the roof or to another corner of the house.

How, then, are these various bits and parts of the house, as represented by simple line orientations and corners, eventually represented as an entire object? Area V4 sends many outputs to higher visual areas in the *ventral visual pathway*, which is important for object recognition (Ungerleider & Mishkin, 1982). The anterior part of the ventral visual pathway consists of the ventral temporal cortex, which is especially important for object recognition.

2.5 Area MT

The middle-temporal area, or what is commonly called area MT (see [Figure 6.10](#)), is important for motion perception. Almost all of the neurons in area MT are direction-selective, meaning that they respond selectively to a certain range of motion directions and do not respond to directions beyond that range (Zeki, 1974; Albright, 1984). Moreover, some of these neurons respond well to patterns of motion (Albright, 1992), meaning that these neurons can integrate many different motion directions and calculate what the overall direction of an object might be. As we will see, the activity in this region seems to be closely related to motion perception and, when activity in this region is disrupted, motion perception may be severely impaired.

2.6 The ventral and dorsal pathways: knowing what and where

The projections from V1 to higher areas in the cortex can be roughly divided according to two major parallel pathways: a *ventral pathway* leading from V1 to the *temporal lobe* that is important for representing “*what*” objects are and a *dorsal pathway* leading from V1 to the *parietal lobe* that is important for representing “*where*” objects are located ([Figure 6.11](#)). This distinction between the ventral and dorsal pathways, sometimes referred to as the *what* and *where* pathways, respectively, is an important organizational principle of the visual system proposed by Ungerleider and Mishkin (1982).

In the ventral pathway, many signals from V1 travel to ventral extrastriate areas V2, V3, and V4 and onward to many areas of the temporal lobe. The ventral or “*what*” pathway is

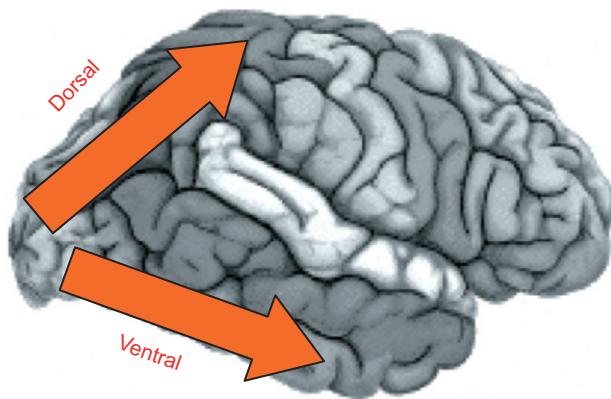


FIGURE 6.11 What and where pathways. The “*what*” pathway includes ventral areas like V4, LOC, and IT; hence it is known as the ventral processing pathway. The “*where*” pathway is typically called the dorsal pathway because it includes dorsal areas like MT and the parietal cortex that are along the top of the brain. These two pathways form a nice way of visualizing the flow of different cortical information. Source: *Squire et al., 2003*.

important for processing information about the color, shape, and identity of visual objects, processing which emphasizes the stable, *invariant* properties of objects. For example, the ventral pathway is less concerned about the exact size, orientation, and position of, say, a coffee mug sitting on a table; instead, its goal is to be able to identify such an object anywhere in the visual field and to be able to tell it apart from other similar objects (e.g., cups, bowls, teapots).

In the dorsal pathway, signals from V1 travel to dorsal extrastriate areas, such as area MT and V3A, which then send major projections to many regions of the parietal lobe. The dorsal pathway is important for representing the *locations* of objects so the visual system can guide actions toward those objects (Goodale & Humphrey, 1998). Consider what is involved in reaching for any object, such as that coffee mug; this type of vision requires detailed information about the precise location, size, and orientation of the object. Without such detailed information, you might reach toward the wrong location, your grasp might not match the size of the handle of the mug, or your hand might not be angled properly for gripping the handle. Areas MT and V3A are important for processing visual motion and stereo-depth, while specific regions in the parietal lobe are specialized for guiding eye movements or hand movements to specific locations in visual space.

While this dorsal-ventral pathway distinction is useful for grouping areas of the brain and understanding how much of the information flows back and forth between visual areas, it should not be taken as an absolute distinction. There is plenty of cross talk between the two pathways. Also, the parietal and temporal lobes send projections to some common regions in the *prefrontal cortex*, where information from each pathway can also be reunited.

2.7 Areas involved in object recognition

Human neuroimaging studies have revealed many brain areas involved in processing objects. These object-sensitive areas, which lie just anterior to early visual areas V1–V4, respond more strongly to coherent shapes and objects, as compared to scrambled, meaningless stimuli. In this section, we will focus on three such brain areas (see [Figure 6.10](#)). The *lateral occipital complex* (LOC) lies on the lateral surface of the occipital lobe, just posterior to area MT. Because this region is strongly involved in object recognition, we will consider it as part of the ventral pathway, even though its position is quite dorsal when compared to other object areas. The *fusiform face area* lies on the fusiform gyrus, on the ventral surface of the posterior temporal lobe. The *parahippocampal place area* lies on the parahippocampal gyrus, which lies just medial to the fusiform gyrus on the ventral surface of the temporal lobe.

2.7.1 The lateral occipital complex (LOC)

The lateral occipital complex seems to have a general role in object recognition and responds strongly to a variety of shapes and objects (Malach et al., 1995). [Figure 6.12](#) shows an example of the neural activity in LOC compared to V1. As the picture becomes more and more scrambled, V1 continues to respond, and even gives a larger response, whereas activity in LOC declines. This shows that LOC prefers intact shapes and objects more than scrambled visual features.

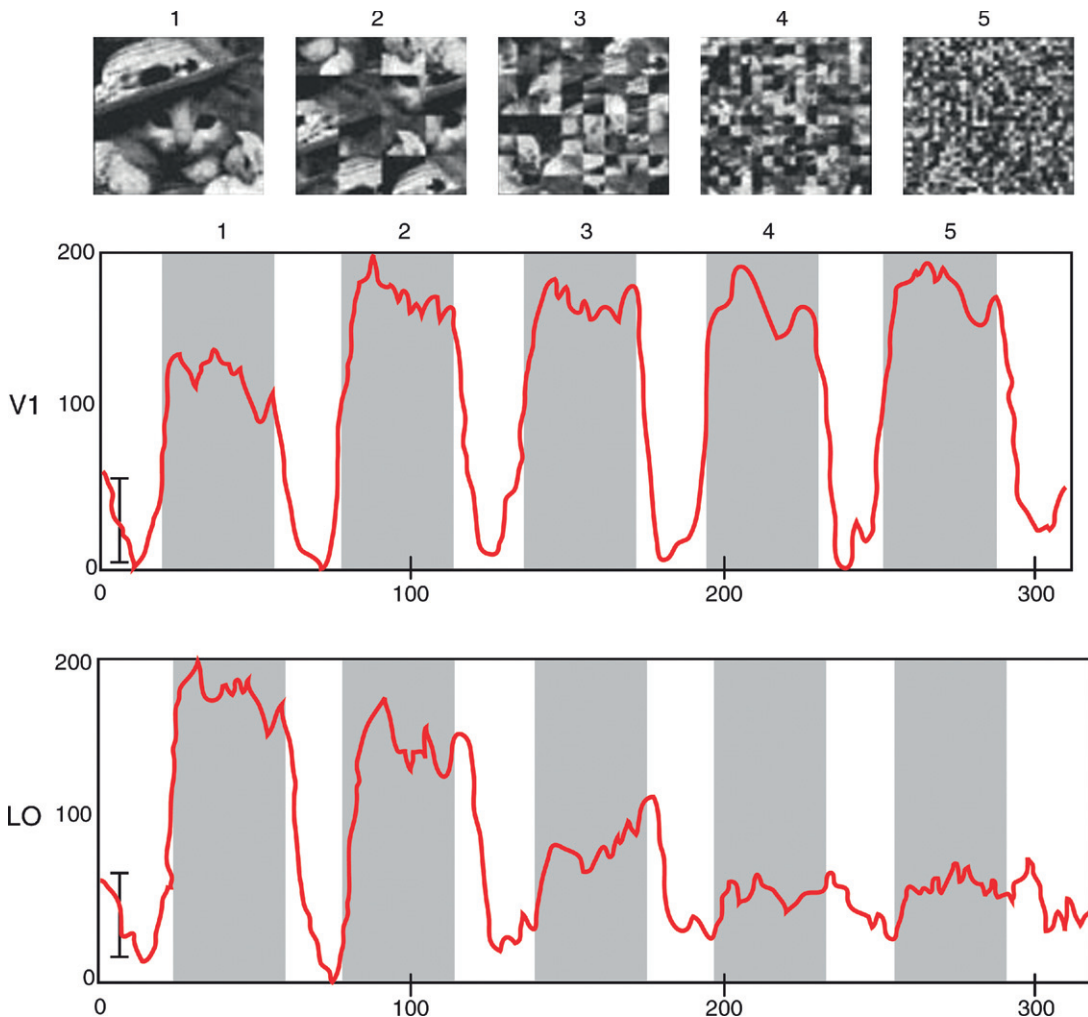


FIGURE 6.12 Neural response from low- and high-level areas. The response of primary visual cortex (V1) and lateral occipital (LOC) to a picture of a kitten at different coherencies. As the picture is scrambled, V1 continues to respond; in fact, it actually increases its response once the image is scrambled. This demonstrates that it is not the image of the kitten that is driving responses in V1 but local patches of luminance and orientation. Conversely, the activity in lateral occipital cortex shows a large response to the kitten, but as the picture is scrambled, the activity in LOC drops down dramatically. This demonstrates that unlike V1, the activity in LOC is in response to the kitten. Source: Frank Tong, with permission.

2.7.2 The fusiform face area (FFA)

Human neuroimaging studies have shown that a region in the fusiform gyrus, called the fusiform face area (FFA), responds more strongly to faces than to just about any other category of objects (Kanwisher et al., 1997). This region responds more to human, animal, and cartoon faces than to a variety of nonface stimuli, including hands, bodies, eyes shown alone,

back views of heads, flowers, buildings, and inanimate objects (Kanwisher et al., 1997; McCarthy et al., 1997; Tong et al., 2000; Schwarzlose et al., 2005). In a recent study, researchers tried scanning the brains of monkeys to see if they might also have a face-selective area in the ventral temporal cortex, and it turns out that they do too (Tsao et al., 2006). The researchers then recorded the activity of single neurons in this face area and discovered that 97 percent of the neurons in this region responded more to faces than to other kinds of objects. Moreover, these neurons were very good at telling apart different identities of faces but poor at telling apart different identities of objects, suggesting they may have an important role in recognizing and telling apart different faces. As we will see, this region seems to be important for the conscious perception of faces (see [Box 6.1](#)).

BOX 6.1

HOW ARE FACES AND OBJECTS REPRESENTED IN THE BRAIN?

Two main theories exist about how the visual system manages to process and recognize objects and faces. The brain could either do it in a *modular* fashion, with distinct modules for processing faces, or the processing could be done in a *distributed* way across multiple areas of the ventral temporal cortex. According to the modular view, object perception is broken down into neural modules, specific areas of the brain that specialize in processing a particular object category. Research suggests that the fusiform face area (FFA) might be a specialized module for the processing and recognition of upright faces (Kanwisher et al., 1997; Tsao et al., 2006). In addition, an area that responds to the presentation of places (e.g., a house) seems also to be a specialized module (Epstein & Kanwisher, 1998). This area has become known as the parahippocampal place area (PPA). This trend for modular representation of objects does not span every object; in fact, it is primarily observed only for faces and places. For example, there is not a banana or shoe area in the human brain.

An interesting twist on the modular hypothesis is the *expertise hypothesis*, which

proposes that the so-called fusiform face area is actually specialized for expert object recognition (Gauthier et al., 2000). We probably spend more time looking at faces than at any other object (especially if you include watching faces on TV). Just stop a moment and think about how much information you can get from all the subtle changes in someone's face when you're talking to him or her, and you soon realize that you are indeed a face expert. It has been proposed that the FFA is responsible for the recognition process of any object we are "experts" at. Research shows that, while looking at pictures of birds, bird experts show somewhat stronger activity in the FFA than do nonbird experts (Gauthier et al., 2000). Whether the FFA is specific for face recognition or any object of expertise, both cases involved a specialized structure that is distinct from regions of the ventral temporal cortex involved in object processing. Look at the two faces in [Figure 6.13](#). Do you notice anything strange? Now turn the book upside down and look again. Now do you see it? This is an example of the face inversion effect. When faces are upside down, we are really bad at identifying them. This is

BOX 6.1 (*cont'd*)

an example of how specialized we are at face perception.

The other hypothesis is that the brain processes faces and objects in a distributed way across multiple areas in the ventral pathway. A study by Haxby and colleagues (2001) demonstrated that regions outside of the FFA still show differential responses to faces, as compared to other types of stimuli. Even if the response difference between faces and different objects is quite small in many of these areas, there is enough information across all of these regions outside of the FFA to tell the difference between faces

and objects. However, neuropsychological evidence of double dissociations between face recognition and object recognition are difficult to explain according to this account. One possible resolution is that the activity of highly face-selective neurons in regions such as the FFA may be important for telling apart subtle differences between individual faces but that more distributed activity patterns outside of these highly face-selective regions are enough for telling apart basic differences between faces and objects and perhaps more obvious differences between faces (e.g., male versus female, young versus old).

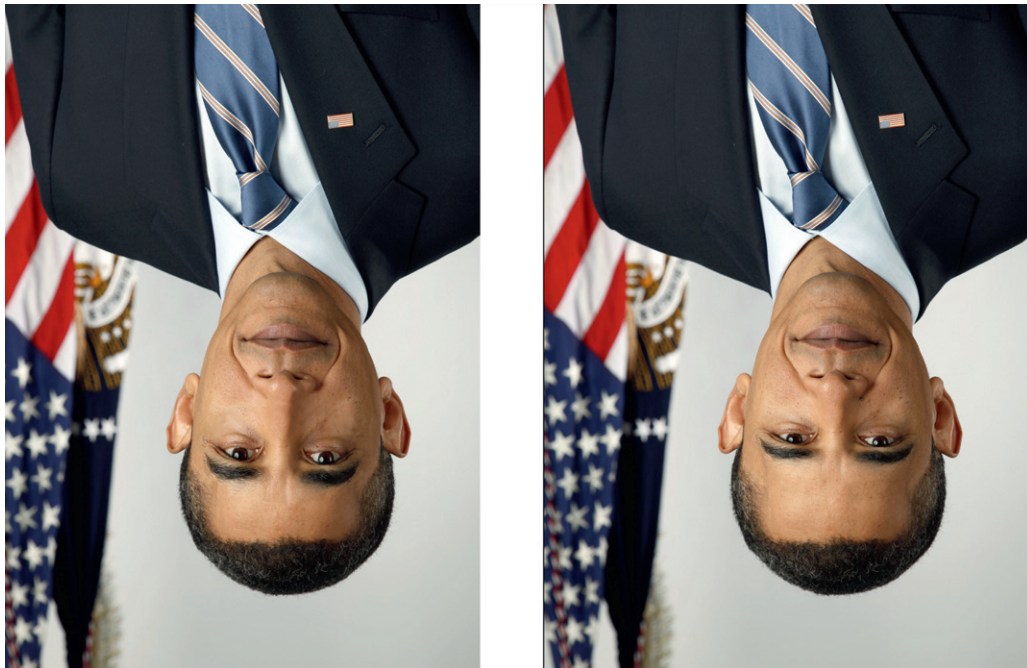


FIGURE 6.13 An example of the *face inversion effect*. Look at these photos of President Obama. Do they look similar to you? Now turn the book/page upside down and look again. Notice how insensitive we are to differences in upside down faces vs. right side up: this is called the face inversion effect.

2.7.3 *The parahippocampal place area*

The parahippocampal place area (PPA) is another strongly category-selective region that responds best to houses, landmarks, and indoor and outdoor scenes (Epstein & Kanwisher, 1998). In comparison, this brain area responds more weakly to other types of stimuli, such as faces, bodies, or inanimate objects. Because this region responds to very different stimuli than the fusiform face area, many studies have taken advantage of the different response properties of the FFA and PPA to study the neural correlates of visual awareness, as we will see later.

3.0 THEORIES OF VISUAL CONSCIOUSNESS: WHERE DOES IT HAPPEN?

So is it possible to say where along this cascade of neural activity consciousness is really happening? Is it possible to point to a particular set of neurons or a particular brain area and say, *"There it is. . . . There is the place in my brain where I am experiencing the visual world in my mind"*?

It turns out that the answer is not so simple, but scientists are gathering important clues. Even if a person's eyes are closed or a person can no longer see because of damage to the eyes or to the LGN, it is still possible for a person to "experience seeing" if electrical stimulation is applied to his or her primary visual cortex. In other words, it is possible to bypass stimulation of the retina and the LGN and induce visual experiences by directly stimulating area V1. Does this effect continue past V1 to higher visual areas? In other words, can one stimulate higher visual areas and induce a visual experience? We don't know the definite answer yet, but so far the answer seems to be "no." V1 seems to be important for our ability to consciously perceive any visual feature, while higher visual areas may have a more specialized role in perceiving certain visual features or objects (Tong, 2003).

Different cortical visual areas seem to play different roles in our conscious visual experience. An emerging view is that many of the same brain areas and neurons involved in processing specific kinds of visual stimuli, such as orientation, motion, faces, or objects, are also involved in representing these types of stimuli in consciousness. Many neurons are more active when a person is conscious of seeing a stimulus than when the stimulus is shown but fails to reach consciousness. So far, there doesn't seem to be any single area in the brain that is solely responsible for consciousness. Instead, many brain areas seem to work together to achieve this remarkable feat. An emerging view is that our conscious experience may reflect the distributed pattern of brain activity involving many visual areas, a kind of dialogue between neurons in early visual areas, including V1, and high-level areas such as those in the ventral temporal cortex and the parietal lobe.

4.0 BRAIN AREAS NECESSARY FOR VISUAL AWARENESS: LESION STUDIES

Studies of people or animals with selective brain damage are important for understanding what brain areas may be necessary for certain kinds of visual awareness—awareness of color, motion, faces, objects, or the capacity to be aware of seeing anything at all! Brain

lesions may be performed experimentally in animal studies, or they may be investigated in humans who have suffered from unfortunate injury to certain parts of the brain, which may result from strokes, tumors, trauma, or neurodegenerative diseases. By studying these patients, it may be possible to understand the neural causes of their impairment, which may inform scientists about brain function and eventually lead to new ways to help treat such impairments.

4.1 Consequences of damage to early visual areas

Different visual deficits can result from neural damage at different levels of the visual processing hierarchy. Damage to the retina or optic nerve of one eye can result in monocular blindness—the loss of sight from one eye. Damage to the LGN, the optic radiations that travel to V1, or V1 itself, can lead to loss of vision in the contralateral visual field (see [Figure 6.7](#)). Damage to a small part of V1 can lead to a clearly defined scotoma, a region of the visual field where perception is lost.

4.1.1 V1 and blindsight

Do lesions to V1 lead to a complete loss of visual function? It is difficult to ask an animal if it is conscious of something or not, but a recent study of monkeys with unilateral V1 lesions suggests that they might not be aware of what they see. In this study, monkeys were able to report the locations of objects in their “blind” hemifield accurately if they were forced to make a choice between two options. However, if they were given the choice of reporting whether an object was presented or not, and an object was sometimes presented in the good hemifield, in the blind hemifield, or not at all, they would fail to report objects presented in the blind hemifield (Cowey & Stoerig, 1995; Stoerig et al., 2002). It is as if these objects were not “seen.”

Interestingly, humans with V1 lesions may show similar above-chance performance, even though they report a lack of visual experience in their blind hemifield. Patient DB had tumor surgery that required the removal of his right V1. Careful testing revealed that he was able to perform visual tasks at above-chance levels, despite his reports of lacking any visual impressions, a phenomenon known as *blindsight* (Weiskrantz et al., 1974). These findings suggest that there can be dissociations between visual processing in the brain and a person’s subjective awareness. Sufficient information was reaching DB’s visual system to allow him to make forced-choice discriminations, but this information was not sufficient to support awareness (Weiskrantz, 1986).

4.2 Extrastriate lesions—damage outside area V1

What happens when extrastriate areas are damaged? [Figure 6.14](#) shows a schematic map of visual areas and corresponding deficits.

4.2.1 Motion blindness

Perhaps because we are so sensitive to seeing motion, it is very rare for brain damage to lead to a complete loss of motion perception. However, there is a striking example of one patient who can no longer perceive motion after suffering strokes leading to large

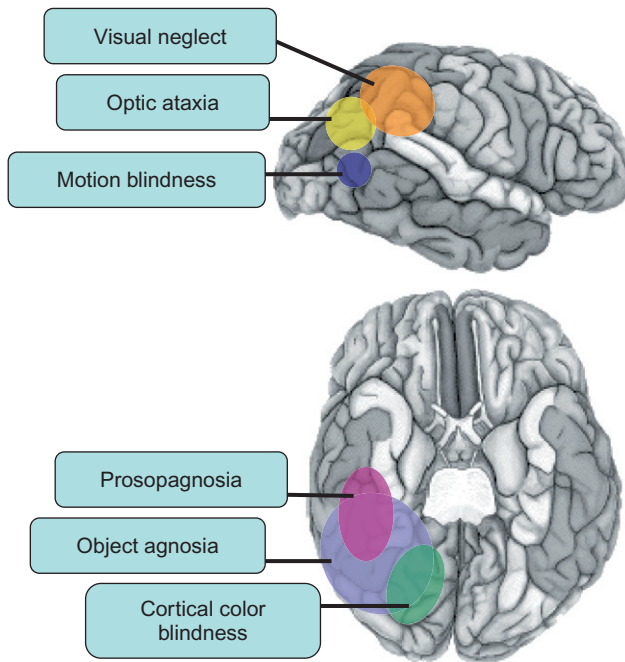


FIGURE 6.14 Visual deficits and brain areas. The areas of the brain in which damage can result in the associated visual deficit. Here, the areas are only shown on one hemisphere, although for some deficits like motion blindness, damage to both hemispheres is required. Source: Frank Tong, with permission.

bilateral lesions that encompassed area MT and extensive surrounding areas. For this patient, the world appeared to be a series of still snapshots, like living in a strobe-lit world. Simple tasks like crossing the street became dangerous, because she could not tell how fast the cars were approaching (Figure 6.15a). Even pouring a cup of coffee became a challenge, since she couldn't tell how fast the liquid was rising, and the cup would overflow.



(a)



(b)

FIGURE 6.15 Color and motion blindness. (a) Damage to motion area MT in both hemispheres can lead to a loss of motion perception: *akinetopsia*. Patients describe seeing multiple still frames instead of smooth motion. This can make simple tasks like crossing the road challenging and dangerous. (b) Damage to color areas in only one hemisphere of the cortex can result in a loss of color perception to one side of visual space. Cortical color blindness is called *achromatopsia*. Source: Frank Tong, with permission.

Other studies have found that smaller lesions just to area MT usually lead to more moderate deficits in the ability to perceive motion, and both patients and animals may also show considerable recovery over time (Plant et al., 1993; Pasternak & Merigan, 1994). So it seems that area MT is very important for motion perception, but other visual areas can contribute to motion perception even when MT is damaged.

4.2.2 Cortical color blindness

Damage to ventral area V4 can lead to cortical color blindness or what is sometimes called *achromatopsia* (Meadows, 1974a; Bouvier & Engel, 2006). Patients report that the world appears to be drained of color, almost like shades of gray, perhaps like the illustration in [Figure 6.15b](#). These patients can still perceive the boundaries between colors but have difficulty with identifying the colors themselves. Achromatopsia is typically associated with lesions that include area V4 and possibly regions just anterior to area V4. Damage to one hemisphere can even lead to selective loss of color perception in the contralateral visual field.

4.3 Damage to ventral object areas

4.3.1 Visual agnosia

Patients with *visual agnosia* have difficulties with recognizing objects because of impairments in basic perceptual processing or higher-level recognition processes. Such patients can still recognize objects by using other senses such as touch, hearing, or smell, so the loss of function is strictly visual. The word *agnosia* can be translated from Greek as meaning “to lack knowledge of,” so visual agnosia implies a loss of visual knowledge.

Here, we will discuss three types of visual agnosia: *apperceptive agnosia*, *associative agnosia*, and *prosopagnosia*. Patients with *apperceptive agnosia* can still detect the appearance of visually presented items, but they have difficulty perceiving their shape and cannot recognize or name them. These patients usually fail at shape-copying tests and may have difficulty copying very simple shapes, such as a circle, a square, or perhaps even a single tilted line. Carbon monoxide poisoning is a frequent cause of *apperceptive agnosia*, since this can lead to profuse damage throughout the occipital lobe.

Remarkably, some *apperceptive agnosics* show evidence of unconscious visual processing of visual features they cannot consciously perceive. Goodale and colleagues (1991) tested an *apperceptive agnosic* patient, DF, who had difficulty reporting the orientation of simple lines or real objects. When asked to report the orientation of a narrow slot cut into the face of a drum, she was unable to report the angle of the slot and made many errors. However, when asked to post a card through the slot, she could do so with remarkable accuracy. Surprisingly, when she was asked just to hold the letter by her side and rotate it to match the angle of the slot, her performance was poor once again and she reported that the slot seemed “less clear” than when she was allowed to post the card. What can account for this behavioral dissociation between DF’s ability to report the angle of the slot and to perform a visually guided action?

Patient DF provides strong evidence to suggest that there are separate pathways for processing “what” an object is and “where” it is with respect to performing a visually guided action. According to Goodale and Milner, patient DF has damage to the ventral visual pathway but intact processing in the dorsal pathway, a claim that has recently been supported by

brain imaging studies (James et al., 2003). They propose that the dorsal system is not only responsible for processing “where” objects are but also “how” actions can be performed toward a particular object, such as pointing or reaching for that object. Apparently, visual processing in the dorsal system is not accessible to consciousness—the patient can’t report the orientation of the slot—yet the dorsal system can guide the right action.

Associative agnosia refers to the inability to recognize objects, despite apparently intact perception of the object. For example, when asked to copy a simple picture, patients with associative agnosia manage to do a reasonable job, especially if given enough time. Dr. Oliver Sacks described a patient who, as a result of brain injury, “mistook his wife for a hat.” The patient had great difficulty identifying objects, even though his vision was otherwise normal, and he could describe the features of what he saw. When presented with a rose from Dr. Sacks’s lapel, the patient described it as “a convoluted red form with a linear green attachment,” but only upon smelling it did he realize that it was a rose. When his wife came to meet him at the doctor’s office, he accidentally reached for her head when he wanted to retrieve his hat from the coat rack (Sacks, 1985). Associative agnosia usually results from damage to the ventral temporal cortex.

Although most patients with visual agnosia will have difficulty with recognizing both faces and objects, there are some remarkable exceptions that have been reported. Patients with *prosopagnosia* are still able to recognize objects well but have great difficulty recognizing or telling apart faces (Bodamer, 1947; Meadows, 1974b). Deficits can be severe; some prosopagnosic patients can no longer recognize close family members or friends and, instead, must rely on other cues such as the person’s voice or clothing to recognize that person. Some patients can no longer recognize their own face in photos or even in the mirror.

What type of brain damage leads to prosopagnosia? Prosopagnosia can result from bilateral damage around the regions of the lateral occipital cortex, inferior temporal cortex, and the fusiform gyrus (Meadows, 1974b; Bouvier & Engel, 2006). In some cases, unilateral damage to the right hemisphere may lead to this impairment. Because lesions are usually quite large and might damage fiber tracts leading to a critical brain region, it is difficult to identify a precise site. Nonetheless, the brain lesion sites associated with prosopagnosia appear to encompass the fusiform face area and extend much more posteriorly.

4.4 Damage to dorsal parietal areas

Damage to the posterior parietal lobe (or superior temporal gyrus) can lead to a striking global modulation of visual awareness called *neglect*, in which a patient completely ignores or does not respond to objects in the contralateral hemifield (Driver & Mattingley, 1998). Patients with right parietal damage may ignore the left half of the visual field, eat just half of the food on their plate, or apply makeup to just half of their face. They may also ignore sounds or touches coming from their left.

This syndrome can resemble a disorder of visual perception. However, neglect happens in the absence of damage to the visual system and can involve multimodal deficits, including motor and tactile deficits. Moreover, when patients are instructed to attend to the

neglected field, they can sometimes respond to these stimuli (Posner, 1980). So this syndrome is more a deficit of *attention* than an inability to perceive stimuli. Without specific cuing, patients find it difficult to perceive objects in their neglected field.

5.0 NOW YOU SEE IT, NOW YOU DON'T!

At any given moment, millions of neurons are firing in the visual part of your brain. The activity of some of these neurons is probably closely linked to what you are consciously perceiving here and now, while the activity of other neurons may be far removed from immediate experience. If scientists could somehow isolate the neurons that closely reflect a person's conscious experience, would this reveal which neurons or brain areas are central to consciousness and which are not? This search is for the neurons that *correlate* with changes in perceptual awareness or consciousness; hence it has been called the search for the *neural correlates of consciousness* or the NCC for short (Crick & Koch, 1995).

The first challenge involves telling apart *stimulus-driven activity* from activity linked to awareness. Not all visual responses are conscious, as we can see from the fact that many visual areas respond well to stimuli even when an animal is anesthetized.

How then is it possible to measure awareness-related activity and separate this from any possible unconscious activity that is driven by the visual stimulus itself? There are many tools scientists can use for this purpose. The next section discusses some of the most popular and useful methods for isolating neurons whose activity correlates with changes in visual awareness.

5.1 Multistable perception

Have you ever been in the dark, perhaps lying in bed, staring at some strange shape across the room? At one moment it might look like a person, then like some strange static animal, then like a marble statue. After racking your brain to identify this mysterious object, you finally hit the light switch and, lo and behold, it's only the dim light catching your jacket on the chair. In this example, when vision was difficult and *ambiguous*, perception did something uncommon: It faltered or alternated between different things. This is an example of *multistable perception*: The jacket on the chair (the physical stimulus) did not change, but your perception of it did! This kind of situation is a valuable tool, since it enables scientists to study changes in visual awareness independent of any changes in the visual stimulus.

There are many examples of *multistable patterns* or ambiguous figures that scientists can use to investigate these neural correlates of consciousness. Patterns that primarily have only two primary interpretations are called *bistable patterns* (Figure 6.16). Try to see if you can perceive both interpretations of each ambiguous figure, the face and the vase and the two views of the Necker Cube. Bistable perception can still occur if you keep your eyes fixed on a single point in the middle of the stimulus. In this case, the image on your retinas—and thus the

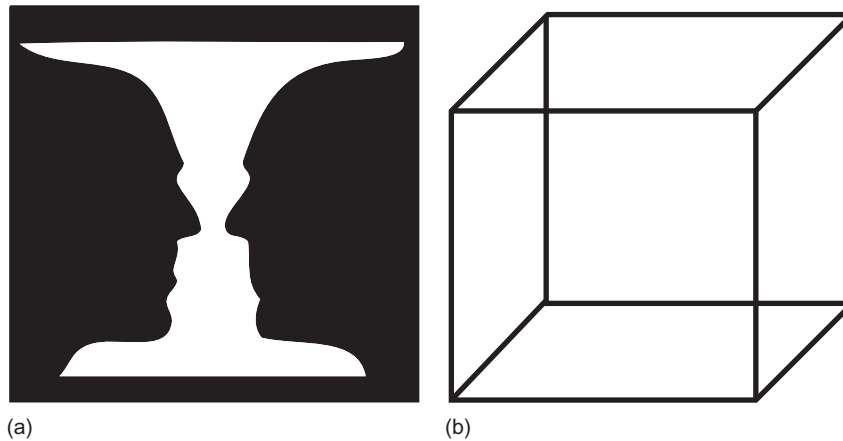


FIGURE 6.16 Bistable figures. (a) After looking at this figure for a while, you will notice that there are two interpretations. One is a central vase; the second one silhouettes of two faces looking at each other. This image is bistable: While you look at it, your perception will alternate between the vase and the faces. (b) This wireframe cube, typically known as the Necker Cube, has two equally likely spatial interpretations. Perception tends to alternate between the configuration of the closest side projecting upward and the closest side projecting downward. Like the vase and silhouettes, this is bistable. This bistability allows a dissociation of low-level stimulation and awareness. The physical pattern does not change, but your awareness of it does!

stimulus-driven activity—is pretty much constant over time, while your perception fluctuates. By looking for brain areas that show activity changes correlated with perceptual changes, scientists can identify the neural correlates of consciousness.

5.2 Binocular rivalry: what you see is what you get activated

One of the most powerful and best-studied examples of bistable perception is a phenomenon called *binocular rivalry*. When two very different patterns are shown, one to each eye, the brain cannot fuse them together as it would normally because they are so different. What then happens is quite striking: Awareness of one pattern lasts for a few seconds, and then the other pattern seems magically to appear and wipe away the previously visible pattern. It is like the two patterns are fighting it out in the brain for your perceptual awareness! If you can get your hands on a pair of red-green filter glasses, then you can experience binocular rivalry by viewing [Figure 6.17a](#). Otherwise, try cross-fusing the two patterns in [Figure 6.17b](#). (To cross-fuse, try letting your eyes cross so the two patterns appear one on top of the other. The dots in the center and surrounding square should fuse. If these demos work for you, you should see one pattern, while the other is completely invisible, almost like closing one eye and then the other.)

What happens in the brain during binocular rivalry? Tong and colleagues (1998) tackled this problem by focusing on two category-selective areas in the ventral temporal lobes: the FFA and the PPA. They used red-green filter glasses to present a face to one eye and a house to the other eye while measuring fMRI activity from these brain areas ([Figure 6.17c](#)). In this study, participants might first perceive the house, then flip to the face and then back

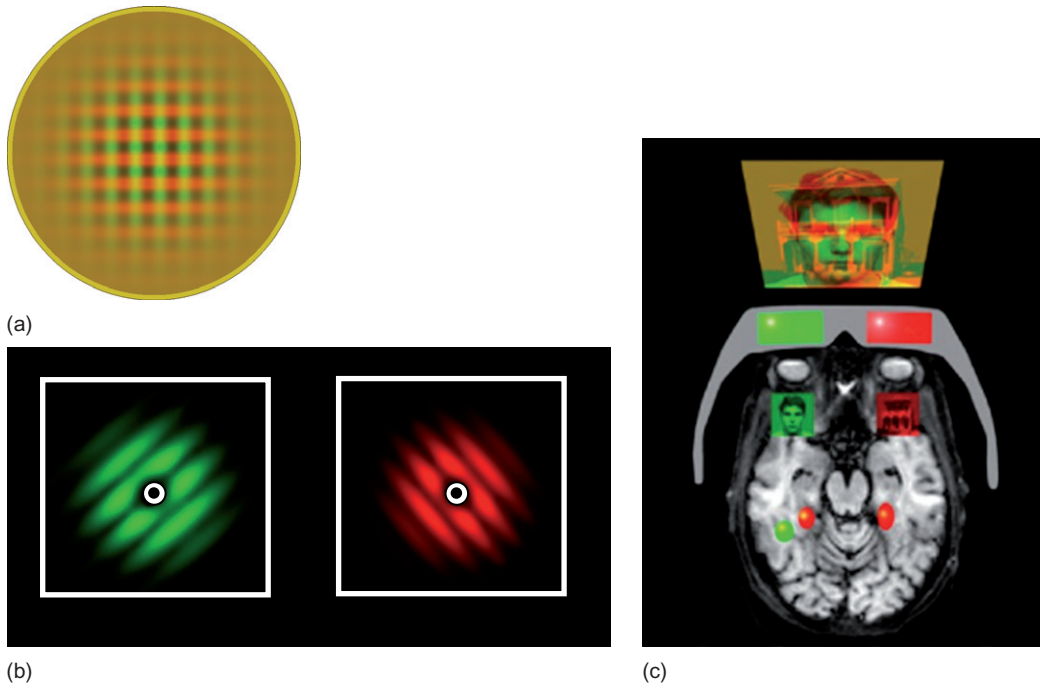


FIGURE 6.17 Binocular rivalry. (a) If you have a pair of red-green filter glasses, this image should produce binocular rivalry. Your awareness should alternate back and forth between vertical and horizontal striped patterns. (b) If you don't have a pair of red-green glasses, try cross-fusing these two patterns. To cross-fuse, you need to cross your eyes so the two patterns line up and appear to be on top of one another. The surrounding squares can help you do this. Line up the square outline and the bull's-eye dot in the middle. (c) Schematic of how Tong and colleagues (1998) used red-green glasses to attain binocular rivalry in the fMRI scanner and the FFA and PPA, where they found activity that correlated with awareness. Source: *Frank Tong, with permission.*

again—as is typical of binocular rivalry (Figure 6.18a). Remarkably, the FFA was active only when subjects reported that they saw the face. Likewise, the PPA was active only when the participants reported that they saw the picture of the house (Figure 6.18b). Next, the researchers tested physical alternations between the two pictures, switching one picture on while switching the other off. The resulting stimulus-driven responses in the FFA and PPA were about the same strength as those measured during binocular rivalry and, surprisingly, not stronger. It seems that the activity in these brain areas closely mirrors what the observer perceives during rivalry and doesn't reflect the temporarily suppressed stimulus that is still activating the retina.

5.3 Visual detection: did you see it?

Another way to separate physical stimulation and perceptual awareness is to get people to do a *visual detection* task. Here, a subject has to detect and say when he or she sees a particular pattern. The researcher makes the pattern harder and harder to see, so on different instances

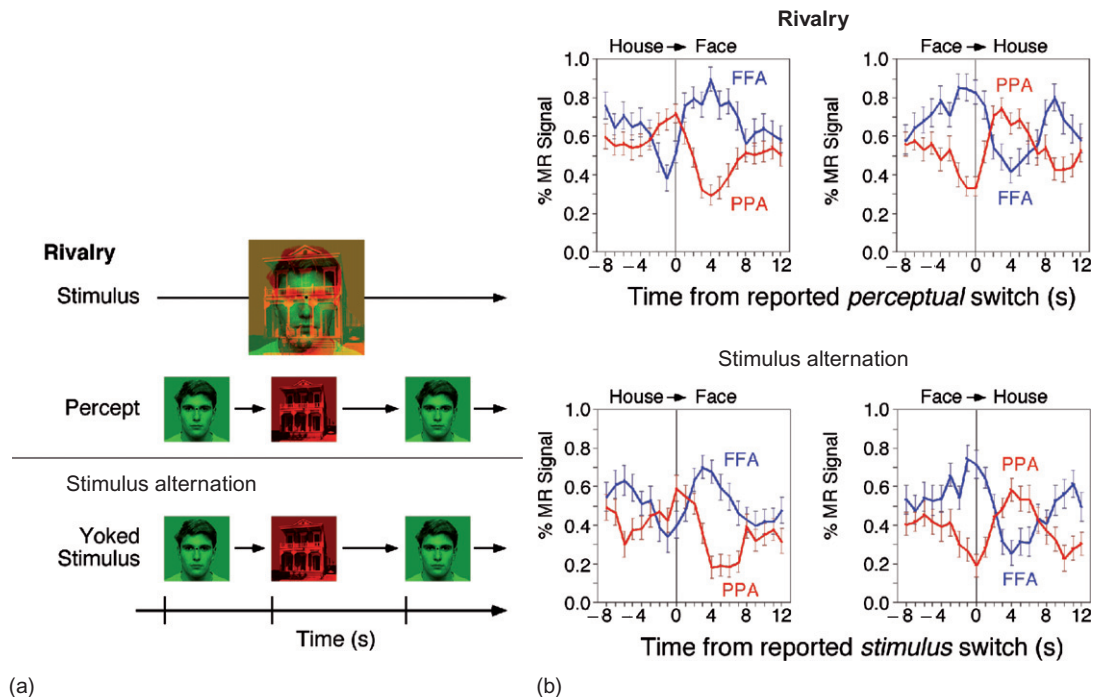


FIGURE 6.18 The stimuli and data from Tong and colleagues (1998). (a) Top panel shows the binocular rivalry condition. Subjects experienced first the face, then the house, then the face, and so on. Lower panel shows a control condition with no binocular rivalry; the images were switched on and off the screen. (b) Top panel shows the fluctuations in activity in both the FFA (blue) and PPA (red) during binocular rivalry. When each image became perceptually dominant, activity in the corresponding area increased. Lower panel shows the neural response in the same areas to the control condition with no binocular rivalry. The alternations in activity in both conditions were around the same size. Source: Tong *et al.*, 1998.

the pattern might be easy to see, while at others times it is almost impossible, and sometimes it won't even be there. Because this task gets difficult, people will get it wrong sometimes. There will be occasions when someone reports seeing the pattern when it wasn't even presented and other times when he or she will miss the pattern and report seeing nothing. When this kind of experiment is done in the fMRI scanner, we can see the pattern of brain activity corresponding to the visual pattern. Also, when no pattern is displayed and subjects report that they don't see the pattern (*true negative*), we don't see that type of brain activity for the pattern. However, what do you think happens when someone gets it wrong? This is the case when no pattern is actually presented, but the subject thinks he or she saw something and so reports, "Yes, the pattern was there" (*false positive*). Interestingly, activity in areas V1, V2, and V3 closely follows what we think we saw. In other words, on trials where a faint stimulus is presented but the subject fails to detect it, activity is much weaker in these areas (Ress & Heeger, 2003). However, if no stimulus is presented, but the subject mistakenly thinks that a faint stimulus was presented, it turns out that activity is greater in V1, V2, and V3 on these trials.

This is another example of how the brain's activity may closely reflect the phenomenal experience of seeing something, even when nothing was actually presented. This is interesting because it demonstrates that it doesn't matter what physical pattern is presented to a person; what does matter is what is happening in the brain!

5.4 Constructive perception: more to vision than meets the eye . . .

If you drive a car, then you probably know what a blind spot is; for the driver it's the area behind the car that cannot be seen in the side- or rear-view mirrors. Our eyes also have a *blind spot* at the back of the retina where the axons of the retinal ganglion cells meet to form the optic nerve as it exits the eye (see [Figure 6.3b](#)). There are no photoreceptors in the blind spot, so we are blind in that area.

It is easy to demonstrate the blind spot. Look at the diagram in [Figure 6.19a](#). Close your left eye, look directly at the cross with your right eye, and move the textbook close to your nose. Then move it slowly away from your face, while keeping your eye fixed on the cross. At the right distance, which should be around 12 inches (30 cm) away from the page, you should notice the dot vanish. As the image of the dot on your retina moves into the blind spot, it disappears!

Hopefully this demonstration worked on you, and perhaps you are thinking, "Wait a minute! If there is a blind spot in my vision all the time, then why don't I see a hole in my vision when I look around at things with one eye covered?" Well, the brain does something remarkable: It actually *fills in* perception of the blind spot. The brain uses the visual information from around the blind spot to infer what should be in the blind spot, and it constructs awareness of what it "thinks" should be there. Filling in at the blind spot is an example of *constructive perception* or *perceptual filling in*.

Another way to demonstrate the filling in can be seen by viewing [Figure 6.19b](#). Move the page around until the gap between the lines is in the blind spot. When each group of lines is abutting the blind spot, what you will see are continuous long lines. The red dot should be replaced by one continuous set of lines. The brain fills in the path of the lines so you don't see the red dot in the gap anymore. This is a case of perceptual filling in; the brain actively creates the perception of a complete object from the separate segments that lie on either side of the blind spot.

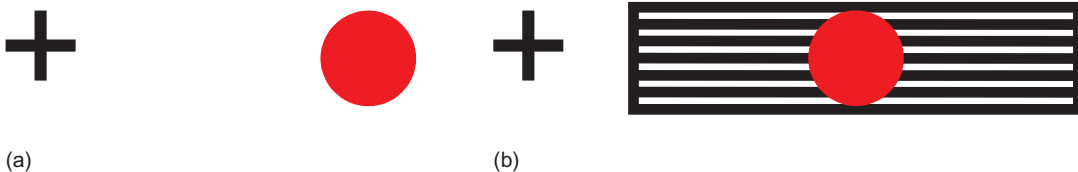


FIGURE 6.19 Demonstrations of the blind spot. (a) Close your left eye, look directly at the cross with your right eye, move the page up close to your nose, and then move it slowly away from your face, while keeping your eye fixed on the cross. At the right distance, which should be around 12 inches (30 cm) away from the page, you should notice the red dot vanish. As the image of the dot on your retina moves into the blind spot, which has no photoreceptors, it disappears! (b) Likewise, notice how the black stripes now fill in; they become joined, and the red dot vanishes. Source: Frank Tong, with permission.

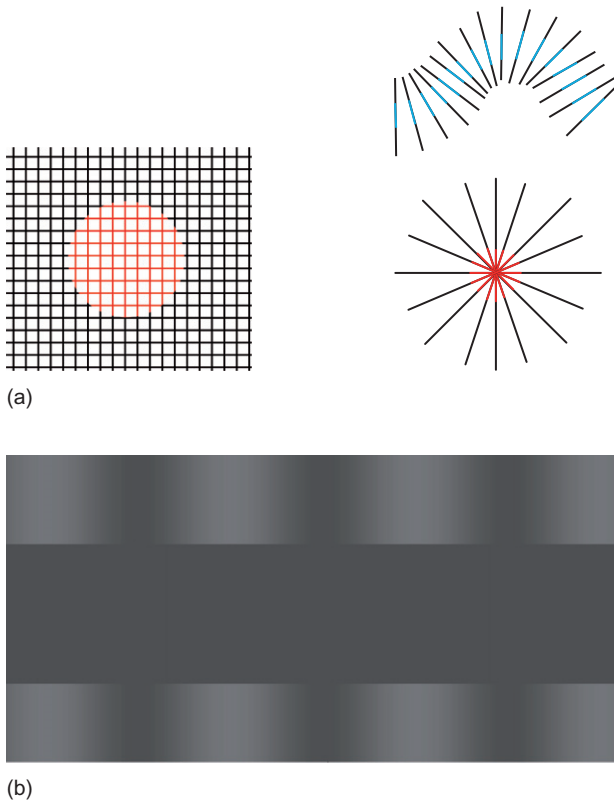


FIGURE 6.20 Demonstrations of perceptual filling in. (a) In these three examples the background is white—it has no color. However, you might notice that the red and the blue tend to fill in, coloring the white background. (b) The light patches and dark patches in the top and bottom panels tend to give the impression of light and dark sectors along the center strip, even though the center strip is a uniform gray. This illusion works much better when moving. Source: Frank Tong, with permission.

Perceptual filling in not only happens in the blind spot, but it also occurs in other parts of the visual field. Notice how the area between the colored lines in [Figure 6.20a](#) somehow appears colored. However, careful inspection reveals that this background area is actually just white—no color at all. This illusion is called *neon color spreading*, and the experience of color here seems to come from constructive filling-in mechanisms at work in the visual cortex. Recent brain imaging studies have found that activity in V1 is greater in corresponding regions where subjects perceive neon color spreading (Sasaki & Watanabe, 2004). This suggests that neurons as early as V1 may be important for perceptual filling in and our experience of color, even illusory colors.

During another type of filling in known as *visual phantoms* ([Figure 6.20b](#)), our visual system can also fill in gaps between two patterns. In [Figure 6.20b](#), you may have the impression of dark bands continuing across the blank gap, even though there is no stimulus being presented there at all. Using moving stimuli can further enhance the visual phantom illusion. When we experience this type of filling in, cortical areas V1 and V2 respond as if a real pattern were being presented in the gap (Meng et al., 2005).

The brain can fill in not only color and patterns but also motion. If you flash a spot of light in one location, then follow it by a similar flash at a different location at the appropriate time, observers

experience the illusion of movement—*apparent motion*. This kind of trick is used all the time in overhead shop signs, and it's the basis for why movies look so smooth and real. If you look at the actual film running through the projector, you will find that there is a series of stills that are flashed onto the screen one after another: The experience of smooth motion is simply an illusion. Recent studies have found that the perceived path of apparent motion is represented by neural activity in V1 (Jancke et al., 2004; Muckli et al., 2005). From the preceding examples, it should be clear that the brain can actively construct perceptual representations, even when there is no physical stimulus presented in a particular region of the visual field. Filling in appears to occur in early visual areas, as early as V1, suggestive that early visual areas may provide the basis for constructive visual experiences.

6.0 SUMMARY

Vision is perhaps our most important sense modality. It is certainly the one that has seen the most research. Over the past decade or so, scientists have learned a great deal about the neural correlates of conscious and unconscious perception and how the disruption of different brain areas can disrupt specific aspects of visual consciousness. A consistent finding is that primary visual cortex seems to be important for the ability to perceive any visual feature at all, while higher brain areas may be important for perceiving *particular* visual features or objects. Future studies will improve our understanding of how the brain gives rise to our subjective visual experiences.

In this chapter, we traced the functional properties of neurons as visual signals travel up from the retina to the primary visual cortex and onward to higher areas in the dorsal and ventral visual pathways. Progressing up the visual pathway, receptive fields gradually become larger and respond to more complex stimuli, following the hierarchical organization of the visual system.

V1 is selective for many visual features, including orientation, motion, and binocular disparity. Damage to V1 can severely impair or eliminate conscious vision, although remaining activity in extrastriate areas may support the ability to detect visual events even without being visually conscious—the condition called blindsight. Extrastriate visual areas (the ones outside of V1) seem to be important for perceiving specific visual features: Area V4 is important for color perception and area MT for motion perception. Damage to these areas may lead to selective impairment in the perception of these higher-level features of the visual world.

Damage to the dorsal pathway can lead to *optic ataxia* (impairments in visually guided actions) or *visual neglect*. Damage to the ventral temporal cortex can lead to impairments in visual perception, object recognition or face recognition. Patients with brain injuries in the ventral and dorsal pathways reveal a dissociation between the conscious perception of basic shapes and orientations and the ability to perform visually guided actions.

In the ventral temporal cortex, some brain regions, such as area LOC, seem to have a general role in object recognition, while other areas, such as the fusiform face area and parahippocampal place area, appear to have more specialized roles. Many studies show that activity in these areas is strongly associated with the conscious perception of objects. Nonetheless, evidence of unconscious processing can be found in many brain areas, including high-level object areas.

7.0 STUDY QUESTIONS AND DRAWING EXERCISES

- For the brain drawing in [Figure 6.21](#):
 - Copy the brain figure. Which way is it facing?
 - Identify the visual regions (labeled) and some of the things they do.
 - Can you color in the dorsal and ventral streams? What is the difference between their functions?
- In [Figure 6.22](#), can you describe what is happening in your own words? What is the cat seeing? Which visual areas are likely to be involved? What kind of neural mechanisms improve the ability of the cat to perceive contrasts and boundaries?

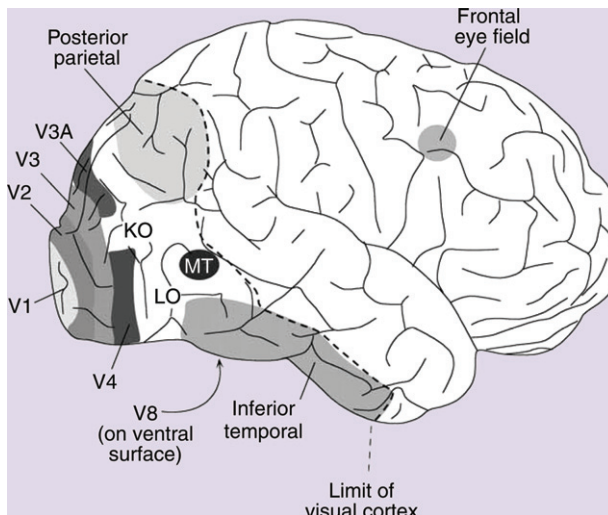


FIGURE 6.21 Visual areas of the human cortex. Source: Rosa, 2002.

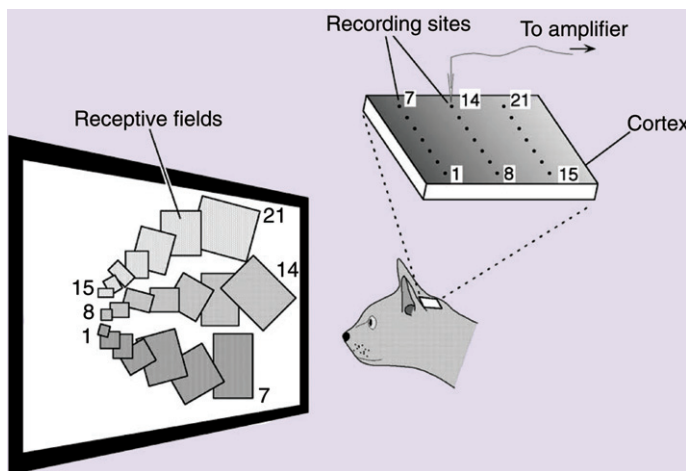


FIGURE 6.22 Recording from the brain of a cat. Source: Rosa, 2002.

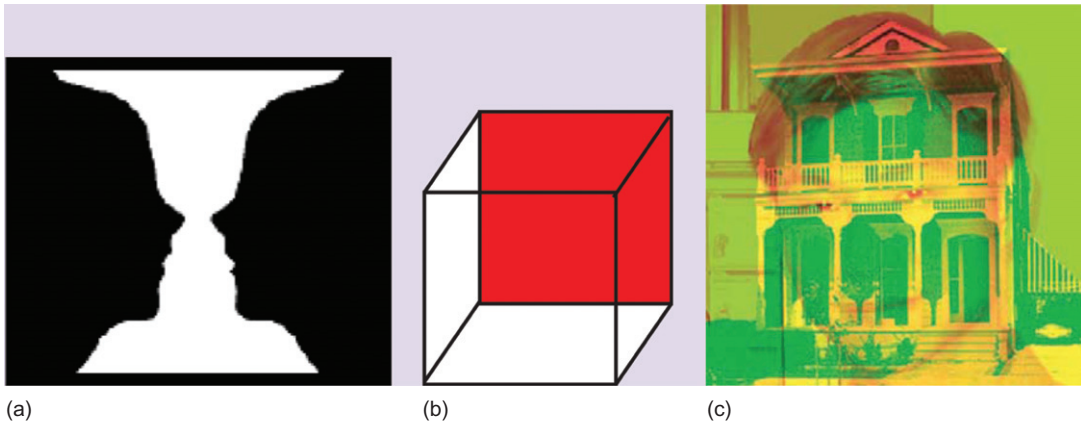


FIGURE 6.23 Visual ambiguities. Source: *a, b. Kim & Blake, 2005; c. Frank Tong, with permission.*

3. For [Figure 6.23](#):
 - a. Draw each figure in color.
 - b. What can we learn from (a)? What parts of the visual cortex are likely to be involved?
 - c. How about (b)? Are different parts of the visual cortex more likely to be involved than in (a)?
 - d. For the third image in the figure, what does the subject in the experiment perceive? Why do the colors look mixed together? What is the purpose of this experiment and what are the results?
4. A question to think about: How can we compare conscious and unconscious visual stimuli?

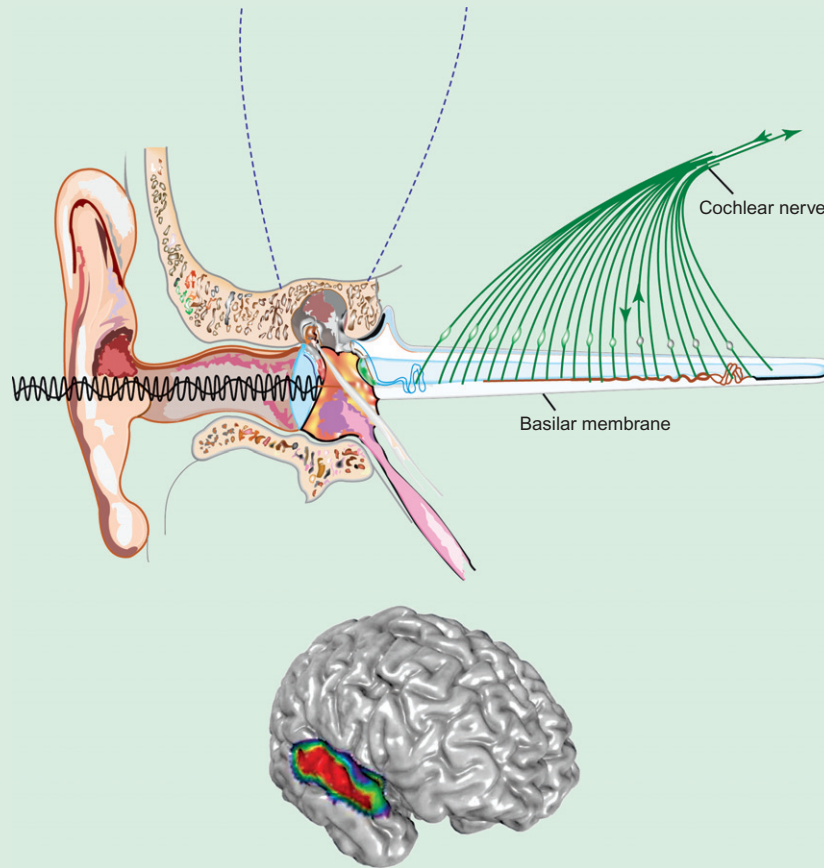
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Sound, speech, and music perception

OUTLINE

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It was very fortunate that, even in Helmholtz's time, the great anatomical discoveries by Corti (and others) had already made it clear that the vibrating tissue most important for hearing is the basilar membrane of the inner ear, because the cells on which the nerve endings terminate are seated on this membrane. . . . The problem of how we hear was reduced largely to a mechanical question: how does the basilar membrane vibrate when the eardrum is exposed to a sinusoidal sound pressure? **Bekesy, Nobel Prize Lecture (online)**



The auditory system really starts deep inside the ear canal at the eardrum. Air vibrations, which are fast compressions and expansions of the air, vibrate the eardrum, which transmits mechanical vibrations that end up triggering receptors (hair cells) located on the basilar membrane. Axons from the receptor cells combine to make up the auditory nerve, which goes through several stages of processing before reaching the cortex (shown in red highlighted regions in the brain figure, above). The auditory system is extraordinarily sensitive, able to pick up even the sound of air molecules in very quiet environments.

Source: *Standring, 2005.*

1.0 INTRODUCTION

This chapter provides an overview of how we hear—from simple sounds, to complex speech, to symphonies. We begin with basic information about how we process sounds: from the ear, through the ascending auditory pathways, to the auditory cortex. Next, we discuss specific types of sound processing such as speech and music perception. As you can imagine, sound perception changes throughout life, for example, as we acquire speech and language as infants and young children. You might have an intuition (and you would be correct!) that the neural systems underlying sound processing may be set up somewhat differently for people who are skilled musicians or for linguists who speak several languages fluently. Therefore, we will discuss the effects of learning and expertise on brain systems for sound processing and how they differ throughout life and across individuals.

1.1 A model for sound processing

Our environment is frequently quite noisy, with many types of sounds reaching our ears at the same time. Think about a large college classroom before a lecture begins: there are the sounds of students' voices, chairs scraping, doors opening and closing, backpacks being unzipped, books being dropped onto desktops. All of these sounds hit our ears at the same time, and yet we have little difficulty in perceiving them as separate events or auditory “objects.” This process is called *auditory scene analysis*, and it forms the basis for understanding how the auditory system decodes a complex listening environment (Bregman, 1990). We will discuss how the auditory system decodes this type of scene. We begin with a functional framework with which to understand auditory system processes and how they interact with other brain systems.

1.1.1 A working framework for sound perception

In [Chapter 2](#), we discussed a modal model for understanding brain processing. The same general concepts hold for auditory processing: sensory (sound) inputs enter the system, and there is a very brief storage (echoic memory) for these inputs ([Figure 7.1](#)). Selective attention allows the system to direct its attention to a subset of the inputs for further processing. At this stage, there are complex interactions between the new inputs and existing memory and experiences, as well as with other sensory systems. The ultimate goal or “action” to be performed is important as well and will affect how information is encoded and stored. It is important to note that this model for auditory processing is not a one-way process, with sounds being decoded, understood, and then stored into long-term memory. There are interactions that occur throughout the encoding of sounds, both within the auditory system itself and across other sensory, cognitive, memory, and motor systems. The anatomy and connectivity of the auditory system reflects this complexity, with multiple stages of processing and neural pathways, including the ascending pathways from the ear to the brain, descending pathways that carry information back to the peripheral system, and many parallel pathways within brain regions and across the two hemispheres.

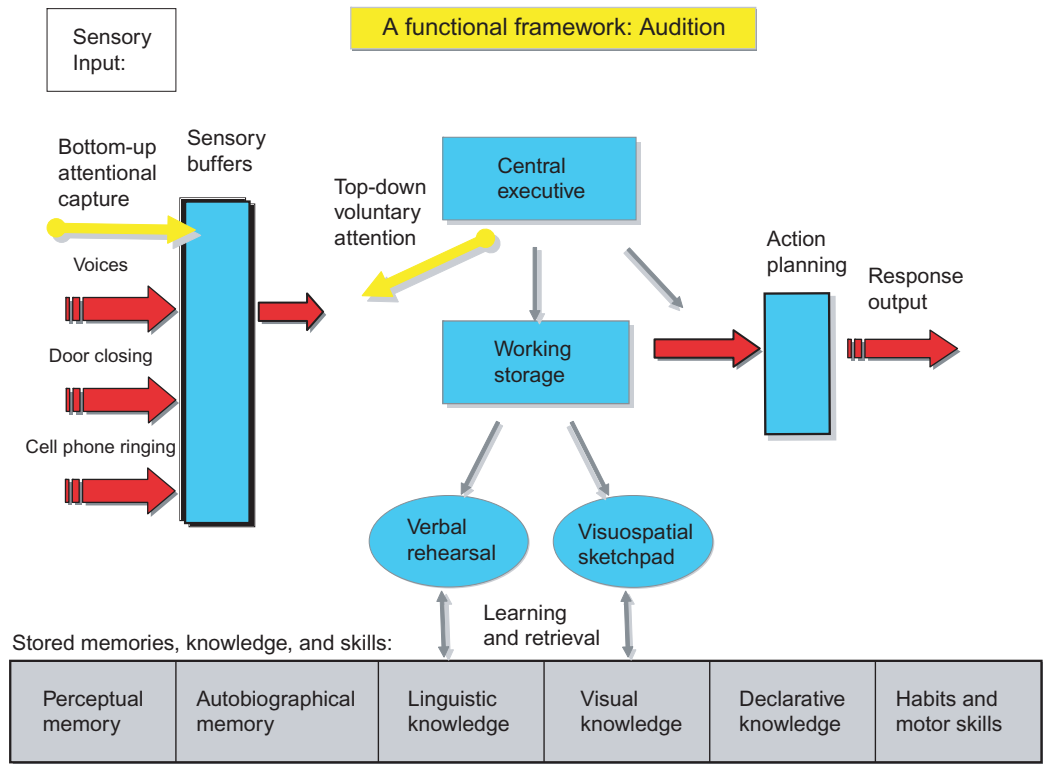


FIGURE 7.1 A functional framework for auditory processing, adapted from the general functional framework presented in [Chapter 2](#). Sensory inputs, such as the sound of someone’s voice or a cell phone ring, enter the system (see red arrows on the left side of the figure). There are early influences from bottom-up and top-down attentional processes (yellow arrows). These inputs make contact with working storage, long-term knowledge, and action systems. It is important to keep in mind that the processes underlying auditory function are highly interactive, with feedforward, feedback, and integrative processes.

1.1.2 Limited and large capacity

Brain processes have both limited and large capacity aspects: this is the case for the auditory system. There are some specific limitations in decoding sound inputs. For example, if you present speech through headphones, it is easy to attend to each word uttered. However, if two different speech streams are presented to the two ears, it becomes a very difficult task to try to attend to each stream. In fact, we selectively listen to one stream or the other (Broadbent, 1982). Thus, there are some limits to the capacity for decoding complex sounds entering the auditory system and a role for central executive function in directing attention selectively to some of the sounds in a complex listening environment. On the other hand, our capacity for learning new sounds or auditory objects (such as spoken words) continues throughout life and appears to be virtually unlimited in capacity. In fact, an average adult’s vocabulary is estimated at more than 100,000 words. The same is true for recognizing new melodies and the voices of new friends and acquaintances. Therefore, while some capacity limits exist in

attending to sounds during perception and encoding, once learned there appear to be virtually no limits regarding the capacity to remember new sound-based items.

1.1.3 Orders of magnitude and levels of analysis

As in other brain systems, auditory processing contains processing units that comprise many orders of magnitude from individual hair cells at the periphery, to single neurons in the auditory cortex, to large-scale neural networks in the auditory language system. The auditory system has been studied at each of these levels of analysis in both human and in animal. In this chapter, we include information that we have learned at each of these levels of analysis. However, a large focus of the evidence presented in this chapter is on what we have learned about auditory processing at the system level from neuroimaging—positron emission tomography (PET), magnetic resonance imaging (MRI), functional MRI (fMRI), magnetoencephalography (MEG), and electroencephalography (EEG)—studies. The advent of noninvasive measures to investigate cortical processing has revolutionized the field of cognitive neuroscience and psychology in general. Previously, we relied on data from animal studies, made inferences from behavioral and psychophysical studies with healthy individuals, or investigated sound and language processing in humans who had suffered brain damage due to injury, disease, or stroke. The capability of investigating brain processes in healthy individuals has provided us with a wealth of new information about sound and language processing. It has also provided us with the ability to investigate brainwide processes in large-scale systems that span multiple brain regions, such as the language system.

1.1.4 Time

Time is a critical aspect of auditory processing: the auditory system differs from the visual system in that all sound processing occurs over time. Nothing “stands still” in sound processing. Speech, the most complex signal that the auditory system must decode, has differences in speech sounds (phonemes) such as /b/ and /p/ that occur on a scale of 20–30 thousandths of a second (milliseconds), and yet our speech perceptual processes decode these transient differences with ease, even in relatively noisy environments (Gage et al., 1998, 2002).

Thus, the speech decoding system has a high temporal resolution of fine-grained and transient changes at the level of the phoneme. However, the speech system also needs to decode information that changes over a longer time span than those contained within phonemes: syllabic stress (such as the different pronunciation of “melody” and “melodic”) is an important speech cue and occurs in a time window of approximately 200 ms. Other key information occurs over 1–2 seconds (1,000–2,000 ms) at the level of a sentence, such as the rising intonation that is associated with asking a question. Thus each of these time windows—20, 200, 2,000 ms—is critical to the accurate decoding of speech, and information extracted from each of these decoding processes must be available for integration in the complex processes underlying the mapping of sound onto meaning (Figure 7.2).

Before we begin our discussion of how the brain processes complicated listening environments, with human voices, complex environmental sounds, and music, we need to discuss some basic principles of sound and hearing. We will begin with the physical features of

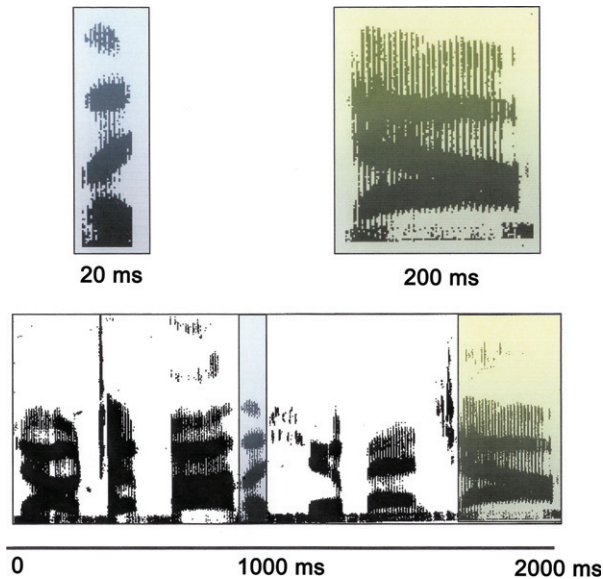


FIGURE 7.2 A spectrogram is a picture of the sound-based features in speech. Time is represented on the x -axis and frequency is represented on the y -axis. The darker shading represents higher intensity. Speech contains harmonic content (formants) at specific regions in the spectral (frequency-based) aspect of the spectrogram. Here we show a spectrogram showing three time scales critical for decoding speech. Upper left: Detail of the transients at the onset of a consonant, with transitions that occur on a time scale of 20 ms. Upper right: Detail of the formants in a syllable that occurs on a time of 200 ms. Bottom: A sentence that occurs on a time scale of 2,000 ms.

sounds and how these features correspond to psychological aspects of sounds. Next, we will step through the processes and stages of peripheral hearing and subcortical feature extraction.

1.2 Sound and hearing basics

1.2.1 Physical features of sounds

How does the human auditory system transform sounds into comprehensible speech or recognizable melodies? Let's begin with how we encode simple sounds at the level of the ear. A physical definition of *sound* is the vibration that occurs when an object moves in space, producing an audible sound. What we hear is not the vibration itself but the effects of vibration in sound waves that move, or propagate, through space and make contact with our ears. The sinusoid is a basic building block of sound that has three main physical aspects: frequency, intensity, and time. The frequency of a sound is the rate of sound wave vibration and is measured as cycles completed per second, or *hertz* (Hz). A sinusoid with 1,000 cycles per second has the frequency of 1,000 Hz. The human auditory system can detect sounds across a wide range of frequencies, estimated at 20 to 20,000 Hz.

The intensity of a sinusoid reflects the amplitude (or displacement) of the wave within its cycle and over time. In [Figure 7.3](#), we show a 1,000-Hz sinusoidal tone in the time domain, with time on the x -axis and displacement or amplitude on the y -axis. A single period of the sinusoid is shown extending from peak to peak. The spectral energy of a sinusoidal tone is limited to a single narrow band, so a 1,000-Hz tone has energy centered only at 1,000 Hz. This is why a sinusoidal tone is frequently referred to as a “pure” tone.

Of course, most sounds that we hear are more complex than a pure tone. A piano chord, a car horn honking, a person's voice—all of these have complicated structures. How do we

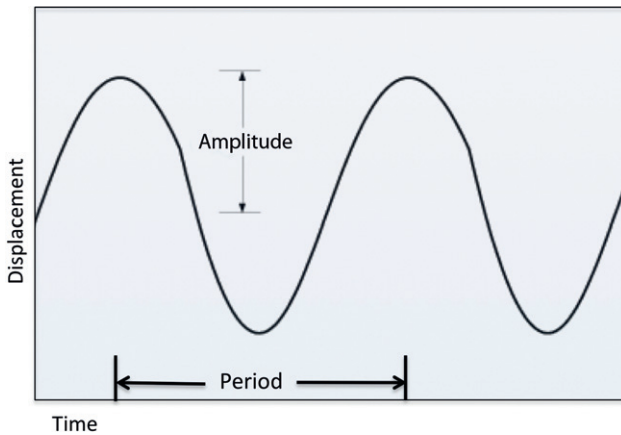


FIGURE 7.3 A sinusoid tone. Time is represented on the x -axis, displacement is represented on the y -axis. The frequency of the sinusoid is based upon the number of repeating periods (single cycle) per second, thus a 1,000-Hertz (Hz) tone has 1,000 cycles per second.

describe these complex sounds in terms of the three physical parameters of frequency, intensity, and time? Joseph Fourier (1768–1830), a Frenchman who lived in the Napoleon I era, developed a series of theorems that describe how even complex signals can be separated into a series of simpler constituent parts through what is now called a *Fourier analysis* (Fourier, 1822). The work of Fourier was advanced by Georg Ohm (1789–1854), who proposed that the separation of complex sounds into simpler sinusoids occurred at the ear in hearing.

While we have mentioned the frequency, intensity, and time of a sound as comprising the basic physical features, sounds have other qualitative aspects. For example, if you heard someone play middle C (261 Hz) on a piano while an oboist played middle C at the same time, could you tell these sounds apart in spite of the fact that they are of identical frequency? Of course you could easily do so, suggesting that there must be many more dimensions in sound quality than just frequency. In this example, the *timbre* or quality of the note helps us distinguish between musical instruments, even when the notes they produce are identical in frequency. Timbre also allows us to distinguish human voices.

1.2.2 A scale for sound intensity

The dynamic range of the human hearing system is extremely broad. We can hear barely perceptible sounds of very low intensity and very loud sounds that actually cause pain. This range has been calculated as ranging from 1 unit of intensity to 1,000,000,000,000,000 (10^{15}) units. This range is so large that it is difficult to deal with using normal numbering schemes. We typically use a logarithmic scale in order to deal more easily with the huge range in units of intensity, the *decibel* (dB) system. The dB scale is a relative (not absolute) scale and is based upon the ratio of two quantities: the relative intensity of a sound based on either the sound pressure level (SPL) in the air where hearing is occurring or based upon the hearing threshold or sensation level (SL) of an individual. (Note: There are many other ratios used in describing hearing. We use SPL and SL here because they are common ratios used to describe sound intensity.) Human hearing ranges from 1 (threshold) to 150 dB SPL (Figure 7.4).

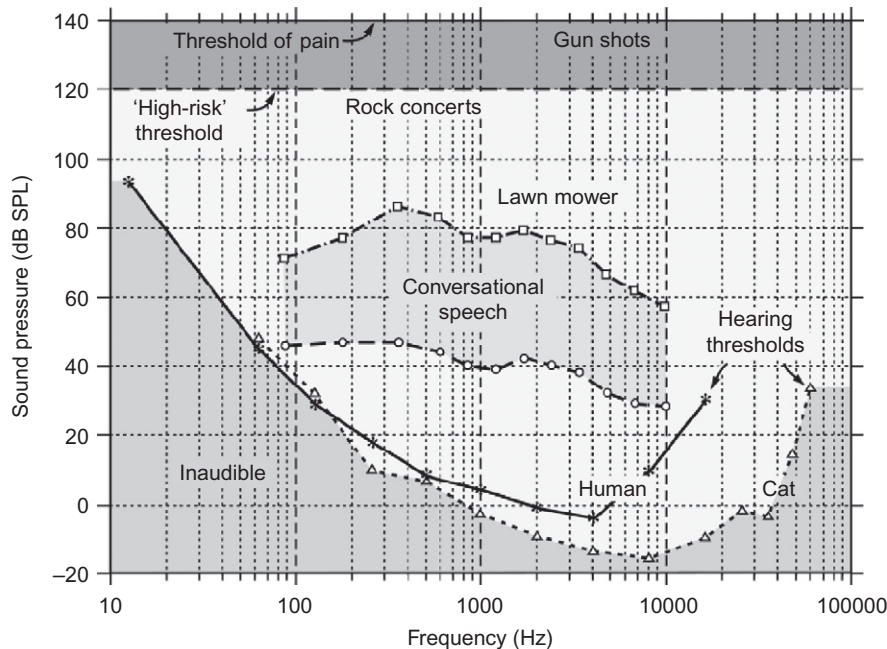


FIGURE 7.4 Hearing threshold and range of hearing for human listeners. Shown also are the ranges of frequency and sound pressure levels of common environmental sounds, including human speech. The most intense sounds are capable of damaging the inner ear receptor organ. The hearing sensitivity of the cat, a laboratory animal commonly used in studies of the peripheral and central auditory system, is illustrated as well. Source: *Adapted with permission from Brugge and Howard, 2003.*

1.2.3 Psychological aspects of sounds

While sounds have physical parameters (frequency, intensity, time) that can be measured with a fine degree of accuracy, how do we know how they are perceived? The physical parameter of frequency, or cycles per second, corresponds to the psychological or perceptual quality of *pitch*. Pitch is a subjective perception, usually described as the “highness” or “lowness” of a sound—for example, the pitch of a person’s voice. We use the physical and psychological terms differently when discussing sound perception. Here’s why: while we may know the frequency of a sound because we have measured the cycles per second, we do not know the precise pitch that an individual experiences. A highly trained opera singer, for example, may have a very different sense of the differences in pitch between closely matched sounds than an untrained individual, even though both have normal hearing. This is also the case for the physical parameter of intensity, which corresponds to the subjective perception of *loudness*. Individual listeners have a wide variety in how they perceive the loudness of sounds, depending on many factors ranging from hearing loss to personal preference. Therefore, it is important when describing sounds to be aware if you are describing the *measured* physical parameters or the *subjective* psychological features.

1.2.4 From the eardrum to the auditory nerve

Let's begin with how sounds proceed from vibrations at the eardrum, through the fluid of the inner ear, to innervate fibers at the auditory brainstem on their way to the auditory cortex. Vibrating objects cause sound waves to move through air. When these sound waves reach the tympanic membrane, or eardrum, they propagate through the middle ear through the mechanical action of the three bones of the middle ear: the hammer, anvil, and stirrup, to the cochlea, the organ of hearing in the inner ear (Figure 7.5).

At the stage of the *cochlea*, in the inner ear, the physical aspects of the sounds are encoded. The traveling wave of sound moves across the basilar membrane from the base to the apex (Figure 7.6). The basilar membrane is topographically organized in a frequency-specific manner, called *tonotopy*, with higher frequencies encoded at the base and lower frequencies encoded at the apex.

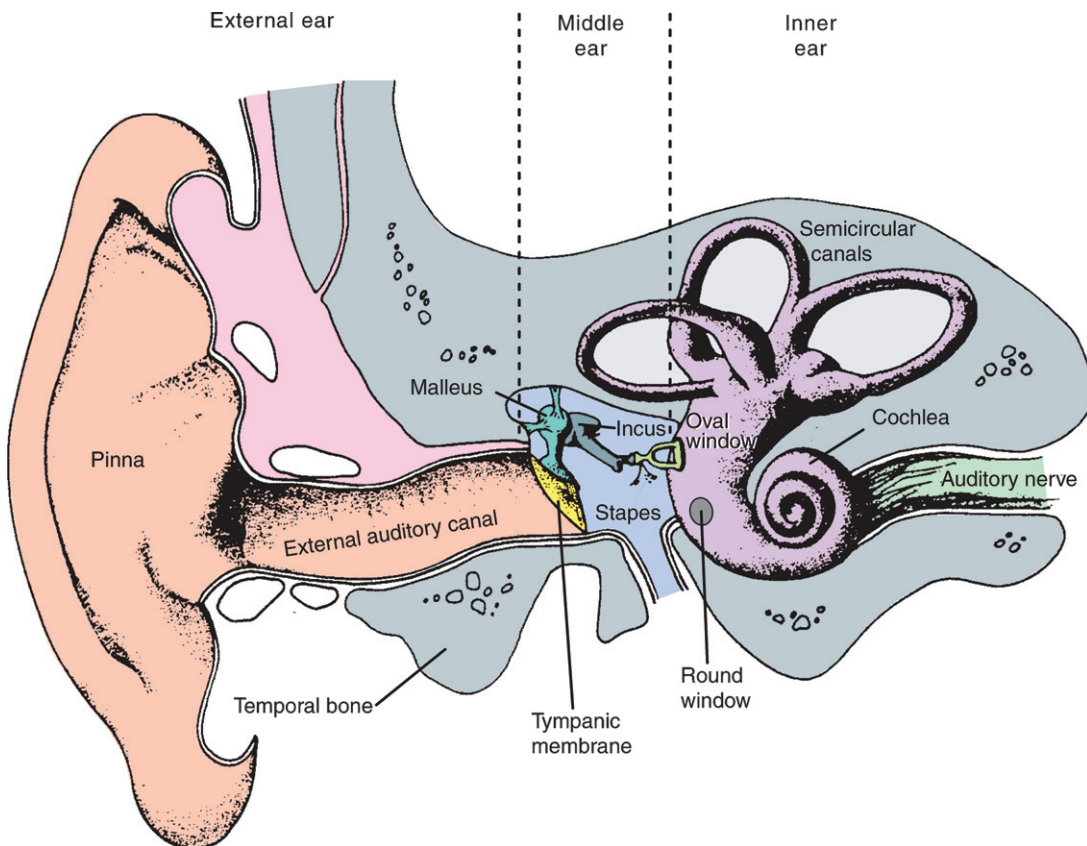


FIGURE 7.5 Drawing of the auditory periphery within the human head. The external ear (pinna and external auditory canal) and the middle ear (tympanic membrane or eardrum, and the three middle ear ossicles: malleus, incus, and stapes) are indicated. Also shown is the inner ear, which includes the cochlea of the auditory system and the semicircular canals of the vestibular system. There are two cochlear windows: oval and round. The oval window is the window through which the stapes conveys sound vibrations to the inner ear fluids. Source: Brown, 2003.

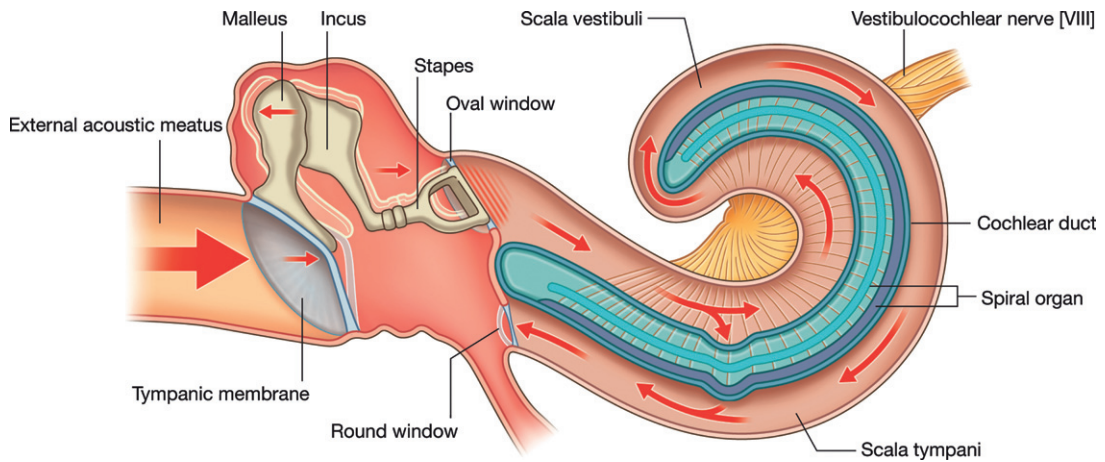


FIGURE 7.6 This figure depicts the transmission of sound, with a perspective view of the cochlea showing the basilar membrane. Note that the red arrows depict sound transmission and are bidirectional. Source: *Drake et al., 2005*.

How is the traveling wave converted to a neural code and transmitted to the brain? Within the cochlea, there are approximately 16,000 sensory receptors called the *hair cells*. The motion of the traveling wave along the basilar membrane sets the tiny hair cells into motion. The peak amplitude of the traveling wave causes maximal bending of the hair cells located in specific places of the basilar membrane, thus encoding the frequency of sounds. This is called the *place principle* of hearing and is based on the theory that the brain decodes the frequencies heard based upon which hair cells along the basilar membrane are activated.

At this stage of processing, the movement of the hair cells produced by the traveling wave of sound is transformed or transduced into electrical responses in fibers of the *auditory nerve* (Kelly et al., 1996). Specific hair cells map onto to specific fibers in the auditory nerve, and these fibers have a *characteristic frequency* to which they are most sensitive.

2.0 THE CENTRAL AUDITORY SYSTEM

The information in sound undergoes many transformations as it ascends to the auditory cortex. The auditory system is comprised of many stages and pathways that range from the ear, to the brainstem, to subcortical nuclei, and to the cortex. The three main divisions of the auditory system are the peripheral system, which we have already discussed, the pathways (ascending to the cortex, descending from the cortex, and parallel pathways across cortical sites), and the central (cortical) system. While each stage and pathway has functional significance in the decoding of sounds, it is important to consider the auditory system as a whole because of the complex interactions across and within its constituent parts.

2.1 Auditory pathways

All sound processing occurs over time. The hallmark of the auditory system is its exquisite temporal resolution for decoding intricate information in sounds (Gage & Roberts, 2000; Gage et al., 2006). One important aspect of the high temporal resolution of the auditory system is the

fast and accurate transmission of sound information along its many pathways. Not only do transient features in complex sounds—such as the harmonic structure of consonants in speech or musical phrases—need to be conveyed rapidly from eardrum to the cortex, but the information from the two ears needs to be combined and integrated in a meaningful way en route.

The *ascending* (afferent) pathways transmit information about sounds from the periphery to the cortex. This pathway is not a simple delivery system but entails significant encoding and recoding of information in the sounds. The neural signal travels from the auditory nerve to the lower (ventral) *cochlear nucleus*. The cochlear nucleus is tonotopically organized. From the cochlear nucleus, the signal continues along the ascending pathway through the lateral lemniscus, inferior colliculus, thalamus, to the auditory cortex (Figure 7.7). This is not a single pathway, but it is complex and includes many computational stages as well as the

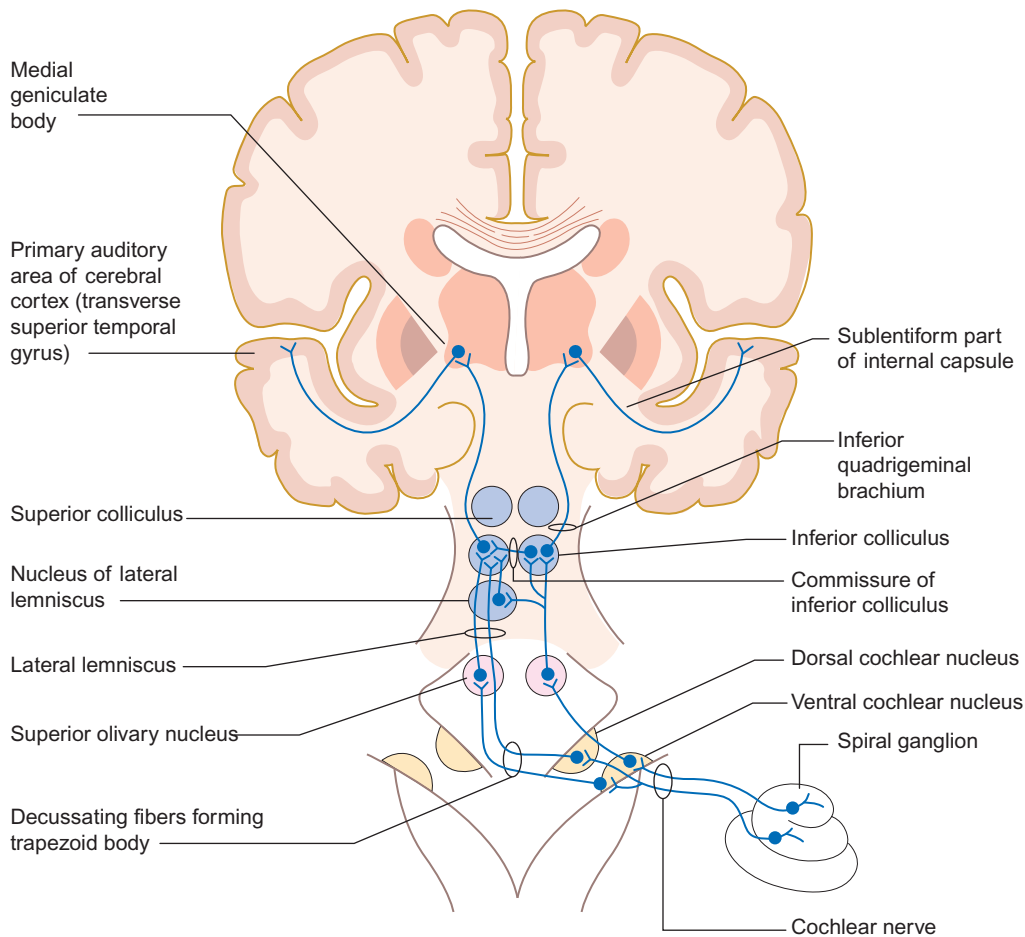


FIGURE 7.7 The human auditory system, showing pathways and subcortical nuclei in the ascending and descending pathways. Source: *Standring, 2005*.

combination of sound inputs from the two ears. A key function of the ascending pathway is to evaluate the information from the two ears in order to localize sounds in space.

The *descending* (efferent) pathways from regions in the cortical and subcortical auditory system cortex to the periphery are under direct or indirect cortical control. Recent research indicates that this control extends all the way to the hair cells in the cochlea! One important function of the descending pathway is to provide “top down” information that aids in selective attention processes and in perceiving sounds in a noisy environment.

The auditory pathways are not just ascending to or descending from the cortex, there are many important connections between the auditory cortices in the left and right hemispheres via the corpus callosum. There are also cortico-cortical pathways that provide integration of auditory processes with other sensory systems, as well as with working and long-term memory processes, and stored memories and knowledge.

2.2 Auditory cortex

The auditory cortex is the region within the cortex specialized for sound processing. It is located in each hemisphere within the Sylvian fissure on the surface of the supratemporal plane and the upper banks of the superior temporal gyrus (Figure 7.8).

Information in sounds is transmitted from the ear to the auditory cortex via the ascending auditory pathways. Along the way, the signal is transformed and recomputed in many ways. The auditory cortex is not the end stage of this pathway but serves as a hub or nexus for sound processing, interacting dynamically with other systems within the cortex, across the hemispheres, and back down the descending pathways to the cochlea.

The auditory cortex is not a unitary brain area but is comprised of several structural (anatomical) areas that differ in their role in decoding sound. Early descriptions of these areas within the auditory cortex were made based on the structure, such as a gyrus within this cortical region, and by underlying neurophysiological features, such as the cytoarchitectonic classification. We discuss our current knowledge about the human auditory cortex in the following, with a description of the structure or anatomy, followed by details regarding the cellular organization and response properties, or neurophysiology

2.2.1 Auditory cortical anatomy

Much of what we know about auditory cortical anatomy comes from work in nonhuman primates (Galaburda & Pandya, 1983). In macaque monkeys, the major regions of the auditory cortex are the core, belt, and parabelt regions. These distinct regions are distinguished by their cytoarchitectural, physiological, and connective properties.

In humans, the primary auditory cortex is located within *Heschl's gyrus* (Figure 7.9) and is roughly analogous to core regions described in nonhuman primates. Typically, the primary auditory cortex comprises only a portion (one- to two-thirds) of the medial aspect of Heschl's gyrus. There is significant variability in the anatomy of Heschl's gyrus both in the two hemispheres and across individuals: Heschl's gyrus is typically located somewhat anterior in the right hemisphere than in the left, and some individuals have more than one Heschl's gyrus.

The auditory cortex extends from Heschl's gyrus in the anterior-inferior direction and the posterior-superior direction along the supratemporal plane and the upper bank of the

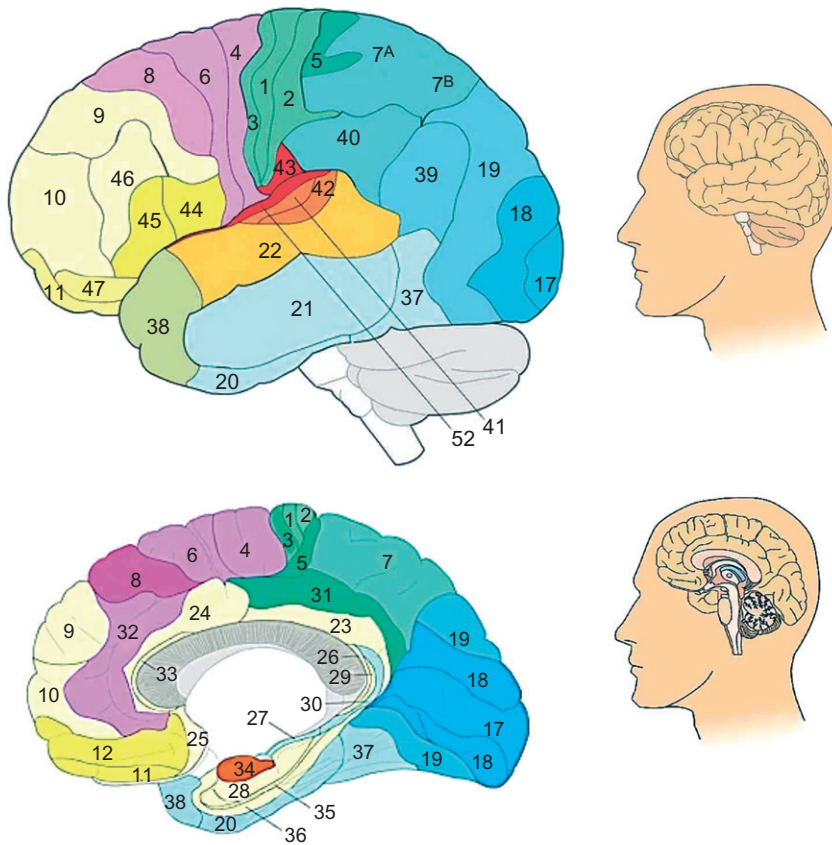


FIGURE 7.8 Top panel: The human brain from a lateral view. Bottom panel: The human brain from a medial view. Colored brain regions are adapted from Brodmann (1909). Auditory and receptive language cortical regions include Brodmann 22, 41, 42, and 52. Note, on the right side of each brain figure we show the brain's orientation within the head. Source: Baars and Fu, with permission.

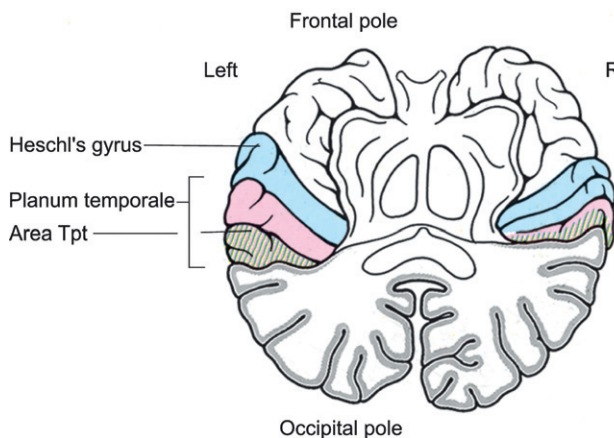


FIGURE 7.9 This drawing of an axial slice of the brain shows regions within the auditory cortex. Note the typical pattern of asymmetries in the left and right hemisphere, with larger planum temporale in the left. Source: Standring, 2005.

superior temporal gyrus. A second important anatomical region in the human auditory cortex is the *planum temporale*, located just posterior to Heschl's gyrus. There are both hemispheric and individual differences in the planum temporale. However, unlike Heschl's gyrus, the differences fall into a general pattern: the *planum temporale* is typically much larger in the left hemisphere than in the right. In fact, the left planum temporale can be up to ten times larger in the left hemisphere in right-handed individuals (Figure 7.9). Planum temporale asymmetries were reported in a series of anatomical studies by Geschwind and colleagues (Geschwind & Galaburda, 1985a, b, c). These scientists noted that language function tends to be lateralized to the left hemisphere. They suggested that the larger left hemisphere planum temporale reflects its role in decoding auditory language. More recent neuroimaging studies, however, have provided a method to specifically test this hypothesis and provide differing views of the role of the planum temporale in sound processing. Just anterior to Heschl's gyrus is the planum polare. This region has not been the focus of much study in humans, and little is known about its role in auditory perception. Posterior to the planum temporale and unimodal auditory areas is Brodmann area 22. This is the area that Carl Wernicke hypothesized played an important role in speech comprehension (Wernicke, 1874/1977). According to Wernicke, this region was not an auditory region per se but formed the language area for speech comprehension processes that were closely related (physically and functionally) to auditory processes. This region is typically referred to as Wernicke's area.

2.2.2 Neurophysiology

Several guiding principles of auditory cortical organization have been established in studies of cats and nonhuman primates. The basic units of organization in the auditory cortex, as in other cortical sensory areas, are neurons, cortical columns, and neural networks. There are several differing types of neurons in the auditory system. These neurons have different response properties for coding frequency, intensity, and timing information in sounds, as well as for encoding spatial information in processes for localizing sounds in space. Most cortical neurons respond to binaural inputs (inputs from both ears), demonstrating the importance of cortical processes for decoding binaural information for sound localization and other complex hearing processes.

Mapping receptive field properties of neurons in the auditory cortex has been the focus of many animal studies. As we mentioned, a large proportion of auditory cortical neurons have inputs from both ears. However, the two ears are not represented in the same way within each hemisphere. In the auditory cortex in the left hemisphere, the right ear, the *contralateral* ear, has a much larger or stronger representation than the left ear, the *ipsilateral* ear. A similar and opposite pattern is observed in the right auditory cortex, with a stronger representation of the left ear versus the right. This general asymmetry for the representation of the two ears in binaural hearing holds true for humans as well (Woldorff et al., 1999).

A central guiding principle for the nonhuman auditory cortex is the *tonotopic* organization. Within the core in the cat auditory cortex, for example, receptive fields of neurons reflect a tonotopic organization in primary (A1) regions that has a mirror image in adjacent (anterior and posterior) core regions. While the basic aspects of neurophysiology are likely similar for humans, the uniqueness of human speech, language, and music perception, as well as the substantially larger regions of the cortex devoted to the auditory cortex in humans, probably mean that there are neurons and networks that are specialized for these complex processes and specific to the

human auditory cortex. For example, although many auditory cortical regions in nonhuman primates reflect a tonotopic organization, evidence for tonotopy has been less robust in human studies and may be limited to the primary auditory cortex and not represent the basic organizational principle in nonprimary auditory areas (Wessinger et al., 2001).

3.0 FUNCTIONAL MAPPING OF AUDITORY PROCESSING

Within the auditory cortex, are there subregions that are specialized for decoding different types of sounds, such as tones versus speech versus music? Or are all areas of the auditory cortex involved in all sound processing, regardless of the class of stimulus? Are sounds processed identically in the left and right hemispheres, or are there subtle differences? Auditory scientists are still unraveling these puzzles. The advent of neuroimaging techniques has provided us with new ways to investigate brain areas for sound processing. Much of this work has been motivated by the investigation of brain regions that may be specialized for decoding speech and language. While neuropsychological studies of patients with brain damage have provided a wealth of information regarding specific language deficits and their correspondence to brain areas, neuroimaging allows the investigation of speech and language processes in healthy individuals. Neuroimaging also provides a way to investigate aspects of auditory function that have not been able to be addressed before, such as what brain areas are involved in imagining a sound versus hearing a sound, and what happens in the auditory cortex while we sleep.

3.1 Primary auditory cortex

We have discussed a hierarchical model for sound processing, developed in animal studies, with neurons in the primary auditory cortex tuned to extract basic physical features in sounds while neurons in the nonprimary auditory cortex are tuned for extracting more complex features. Recent studies in humans have provided evidence that this hierarchy is present in human auditory function, with basic features in sounds encoded in the primary auditory cortex and more complex information in sounds encoded in the planum temporale (Wessinger et al., 2001). This area of investigation is still in its early stages, so we must treat these initial findings with a bit of caution until we have learned more.

3.2 The role of the planum temporale in sound decoding

The prevalence of planum temporale (PT) asymmetry and its location in auditory areas close to Wernicke's area for speech comprehension motivated the hypothesis that PT was the site for auditory speech and language processing (Geschwind & Levitsky, 1968). This idea has been supported by neuroimaging studies investigating the functional role of PT in speech perception. However, neuroimaging studies of PT response to different classes of speech and nonspeech sounds provide evidence that the functional role of PT is not limited to speech sounds. These findings have resulted in a new assessment of the role of PT in sound processing. In a recent review of the functional neuroanatomy of language, Hickok (2009) points out that it is perhaps not surprising that the PT seems to respond to so many classes of sounds and

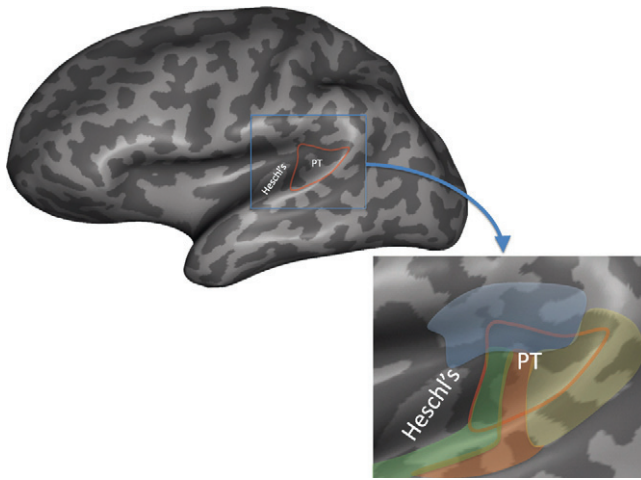


FIGURE 7.10 Just what role does the PT play in sound and language perception? Cognitive neuroscientists are still assessing the PT's role in auditory processing. A recent review of the functional neuroanatomy of language by Hickok (2009) shows that the area we refer to as PT is likely not a unitary functional region at all. If you look at the PT in terms of its cellular (cytoarchitectonic) structure and organization, then you will see that within the anatomical bounds of this region lie four distinctly different fields (shown in green, red, yellow, and blue). These differing fields likely correspond to differing functions performed within this area and may explain why PT is activated in so many neuroimaging studies for a wide variety of tasks and stimulus types. Source: *Hickok, 2009.*

for such a wide variety of tasks. If you look at the PT in terms of its cellular (cytoarchitectonic) structure and organization, then you will see that within the anatomical bounds of this region lie four distinctly different fields (Figure 7.10). These different fields likely correspond to different functions performed within this area and may explain why PT is activated in so many neuroimaging studies for a wide variety of tasks and stimulus types.

3.3 Cortical auditory “what” and “where” systems

The central role of the auditory perception system is to extract information from the listening environment in order to determine what is happening around us. Consider again the large college classroom where doors are opening and closing, students are talking, backpacks are being unzipped, and books are being dropped on desktops. All of these sound events are happening at the same time and are overlapping in frequency and intensity. How does the auditory system decode the individual auditory “objects” such as a friend’s voice, a door shutting, and a cell phone ringing? To accomplish this, the auditory system must keep track of many aspects of the complex auditory scene: *where* sounds are occurring in space and *when* sounds occur (are they simultaneous, or does one sound precede another?) to determine *what* the sound represents in terms of known auditory objects, such as speech or music or new auditory objects to be learned. Of course, these perceptual tasks are not limited to the auditory system but make contact with other sensory systems as your brain integrates what you hear with what you see, feel, and smell. These tasks also interact with your memories and learned information already stored regarding auditory objects that have taken a lifetime to develop.

3.3.1 “Where” system: sound localization

Knowing where a particular sound is coming from is quite useful in decoding the auditory scene, but, of course, it is also critical for survival—allowing us to jump out of the way of an oncoming car or to duck when we hear a loud noise. How does the brain locate sounds in space? Sounds are always changing in time, and the mapping of auditory space is a complex

one. Here is how it works: when a sound occurs, it will likely be off to one side or the other of you. It could also be behind you. In order to determine where the sound is in relation to you, your auditory system must make a very quick determination of the sound's arrival at the two ears. Two basic types of cues are used when our system localizes sound. The first is the *interaural (between ear) time difference*: the difference in time between a sound reaching your left ear versus your right (Figure 7.11a). A second important cue for localizing sounds is the *interaural level difference*. This is the small difference in loudness that occurs when a sound travels toward the head from an angle. The head produces a "sound shadow," so sounds reaching the far ear are somewhat quieter than the near ear, and the absolute level differences depend on the frequency of the sound (Figure 7.11b).

Thus sound localization processes rely on the basic notion that if a sound occurs to the left of you, it will make contact with the eardrum of the left ear slightly before the right ear, and it will be slightly louder in the left ear than in the right. The actual computations that produce sound localization functions involve complex algorithms called *head-related transfer functions* to calculate the location of sounds in auditory space.

While most auditory cortical neurons respond to inputs from both ears, the response is asymmetric, with a stronger representation of information from the contralateral ear compared to the ipsilateral ear. Is there a similar effect for attending to different sides of auditory space? Early investigations by Hillyard and colleagues (1973) provided evidence that there is. Using event-related potentials (ERPs), Hillyard reported a predominant N1 larger response for the attended ear in the contralateral cortex. More recent neuroimaging studies have also provided a way to investigate the effects of selectively attending to auditory space,

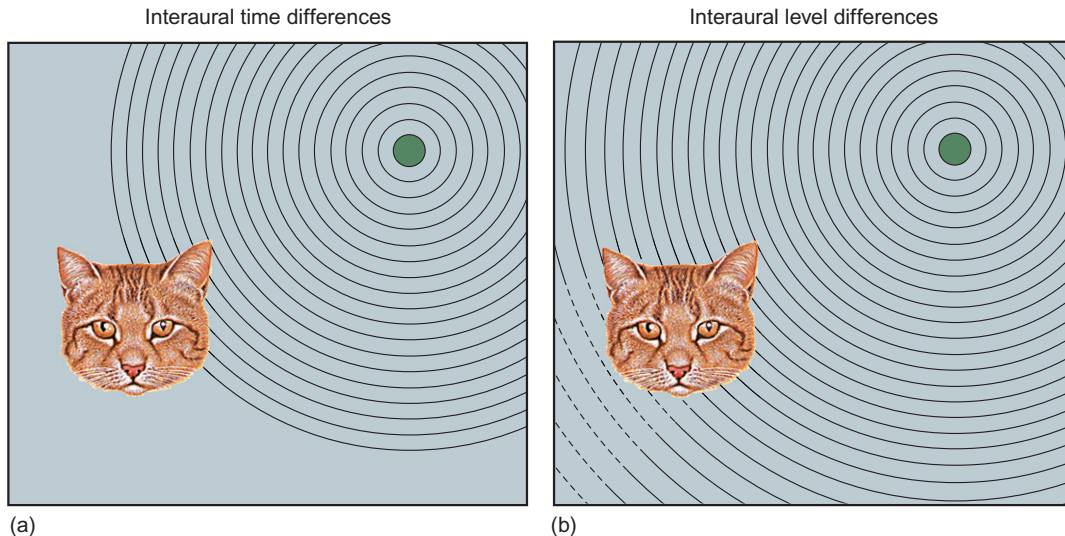


FIGURE 7.11 A schematic drawing of the two cues for binaural sound localization. The sound source is shown as a solid dot to the right of the cat's head. The sound waves produced by the sound are shown as concentric lines. (a) *Interaural time differences* result because it takes the sound waves longer to travel to the ear away from the sound source. (b) *Interaural level differences* result because the head forms a "sound shadow," which reduces the level (loudness) of the sound at the ear that is more distant from the source. Source: Brown and Santos-Sacchi in Squire et al., 2008.

confirming the earlier findings by Hillyard with different methodology (Tzourio et al., 1997; Woldorff et al., 1999). These results demonstrate the powerful role of attention in the auditory system.

3.3.2 “What” system: auditory object recognition and scene analysis

In this section, we discuss the learning processes associated with forming mental representations of auditory objects, as well as those for decoding complicated listening environments. Let’s begin with auditory objects.

The next step is understanding *what* you are hearing. To accomplish this, the auditory system must decode sounds “online” as they occur in order to form a percept of a sound event or auditory object. These objects are learned over time as we grow from infant to child to adult, and they change with experience throughout our lifetime. Auditory objects can take many shapes, similar to visual objects, and vary widely in complexity from a simple computer alert chime, to the slamming of a car door, to a friend’s voice, to a symphony. It seems that the brain has a nearly limitless capacity for storing and retrieving auditory objects. Auditory objects are organized into categories, such as human voices, musical instruments, and animal sounds, that aid us in decoding learned objects as well as learning new ones. Over time, associations are formed between learned auditory objects and coinciding inputs from other sensory systems, and these different sensory memories become integrated in the conceptual representation system. Early work on describing how these sensory inputs are experienced and combined to form conceptual knowledge was provided by Carl Wernicke (1874/1977), who proposed that with experience, when you hear the sound of a bell, you will recognize it as such, and the sound of the bell will also bring to mind (activate) the visual features of a bell, the feel of a bell, and so on.

Because language is uniquely human, it is probably not surprising that there have been many investigations into how the brain decodes speech. We will discuss these later in this chapter. For now, let’s focus on how the brain decodes nonspeech sounds such as environmental sounds. Here we highlight a recent study by Lewis and colleagues (2004), who investigated brain areas for recognizing environmental sounds (e.g., the sounds of a doorbell, a hammer pounding a nail). Results are presented in [Figure 7.12](#): the key finding was that auditory areas in the superior temporal gyrus were activated by both recognized and unrecognized (reversed) environmental sounds. However, recognized sounds also activated regions in the superior temporal sulcus and the middle temporal gyrus (MTG) in both hemispheres. These results are interesting in light of previous investigations of the functional processes of the MTG. The regions identified in this study partially overlap with semantic systems and with areas that have been reported as important for recognition of visual objects such as tools. During the process of learning an environmental sound, it is likely that the sound of a hammer will be heard at the same time movement of the hammer is seen. Thus the sound and the sight of hammering are likely to be linked during the process of learning. Lewis and colleagues propose that this is the case and that the MTG region is a likely candidate for the brain region for this type of object recognition processing.

The results of the study by Lewis and colleagues (2004) are in good accord with earlier studies of individuals with brain lesions who suffered from auditory agnosia, the inability to recognize auditory objects. Cases where the patient suffers from a specific (“pure”) deficit for recognizing environmental sounds, while leaving speech recognition intact, are rare. The investigations of the cases that do exist have reported a complex location of lesions,

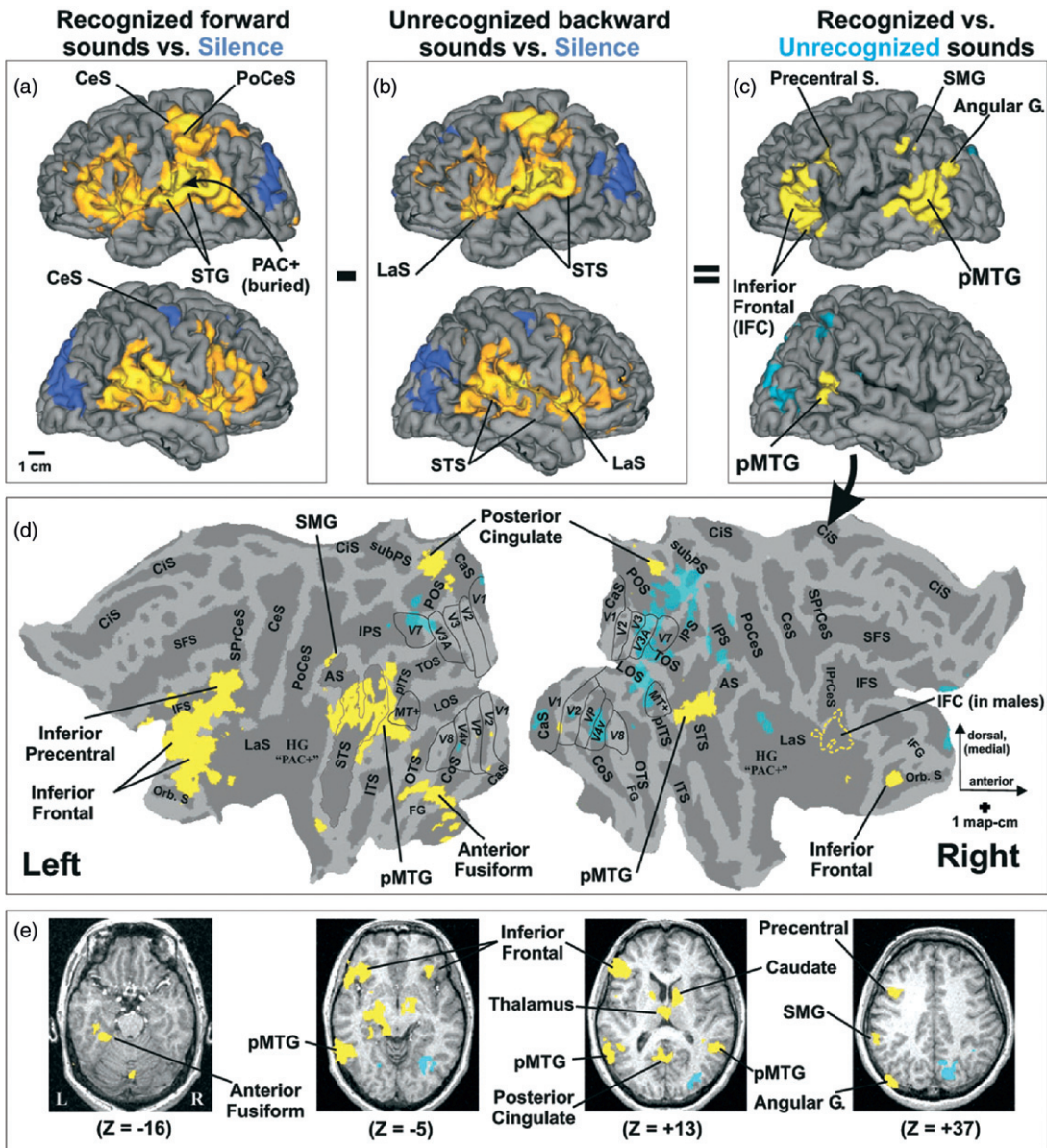


FIGURE 7.12 Brain regions involved in environmental sound recognition. Yellow hues show group-averaged activated regions, and dark blue shows relative decreases evoked by (a) recognizable, forward sounds relative to silence or (b) the corresponding unrecognized, backward sounds relative to silence. (c) Data from (b) subtracted from (a), revealing regions preferentially involved in recognizing sounds (yellow) versus not recognizing the corresponding backward-played sounds (light blue), both relative to silence. (d) Flat maps showing data from (c). The left superior temporal sulcus is outlined in gray for clarity. (e) Axial sections of data from (c) displayed on the brain of one subject. Source: *Lewis et al., 2004.*

with reports of left hemisphere damage, right hemisphere damage, or in some cases bilateral damage (see Clarke et al., 2002). The results of Lewis and colleagues, showing auditory object recognition-related activity in several areas in both hemispheres, provides evidence that the neural substrates of auditory environmental object perception are likely complex and include multiple regions in both hemispheres. This work is an example of how the results of lesion studies inform scientists using neuroimaging techniques to investigate complex cortical processes.

We have described how a sound is decoded by the auditory system to be recognized or learned as an auditory object. This process seems relatively straightforward when you consider a situation where a single sound event occurs in a quiet environment. But how is this perceptual task accomplished in noisy environments, with complex sounds that occur simultaneously in time, with overlapping frequencies, and possibly coming from the same spatial location? How does the auditory system distinguish them as separate sound events? This perceptual task—called the “cocktail party problem” (Cherry, 1953)—has been the subject of many investigations of auditory perception from a theoretical perspective to understand how the auditory system extracts information from complex signals, as well as a practical perspective in designing speech recognition systems. Bregman (1990) provided a model to describe how the auditory system segregates the many different signals in a noisy environment. The four elements in this model are as follows:

1. The source
2. The stream
3. Grouping
4. Stream segregation

The *source* is the sound signal itself. The *stream* is the percept related to the sound. This distinction between the physical signal and the related perception is analogous to the relationship we described earlier in this chapter between the frequency (in Hz) of a sound and the pitch perceived by the listener. *Grouping* refers to how the signals are perceptually combined to identify and maintain attention to some aspects of the auditory scene (such as listening to one friend’s voice in a crowd of people). Perceptual grouping processes create the stream. There are two basic types of grouping. One is *simultaneous grouping*, where if two or more sounds have common onsets and offsets, they may be grouped together. Think of a choir or an orchestra: you will not typically hear each individual voice or instrument but will group them into a single stream due to the beginning and ending of their music together, as well as their shared spatial location. The other is *sequential grouping*, which refers to the process in which features or properties are shared across sounds that occur over time. An example of this grouping process is if you are listening to a professor lecture and someone in front of you coughs. The stream coming from the professor is interrupted by the cough, but you will likely not notice an effect in hearing what is being said. *Stream segregation* uses the grouping processes to segregate separate auditory objects or events into streams.

How does the brain perform auditory scene analysis? Investigations of the neural substrates of perceptual organization have led to the formation of several theories of how and where perceptual streaming is decoded. One view holds that auditory stream segregation involves the primary auditory cortex and that the underlying mechanisms for this segregation involve neural suppression of information not contained within an auditory stream (Fishman

et al., 2001). A second view holds that auditory stream segmentation exploits cortical change detector mechanisms in detecting aspects of the auditory scene that are not part of a single stream (Sussman, 2005). According to this view, an individual auditory stream is detected based on the acoustic aspects of the auditory sound, such as its frequency and location in space. Once these characteristics are formed into a neural representation of the stream, inputs that do not match this stream are detected using auditory cortical change detection mechanisms. A third view is that the perceptual organization processes take place in an area of the cortex that is thought to underlie binding processes for visual and somatosensory input, the intraparietal sulcus (Cusack, 2005). In this view, the perceptual organization of multiple auditory streams occurs external to the auditory cortex in neural territory that is implicated in the multimodal cortex (Figure 7.13).

3.3.3 “What” and “where” processing streams

There is a large and growing body of evidence that cortical networks for decoding what and where information in sound are processed in separate (but highly interactive) processing streams in the human brain. Recent neuroimaging studies have investigated processing of where and what information and have shown differing patterns of activity for decoding this information. In a recent review article, Scott (2005) provides a summary of findings to date and provides hypothesized brain regions for “what,” “where,” and “how” processing streams in the human brain (Figure 7.14). However, the functional mapping of cortical auditory processing streams remains an ongoing investigation.

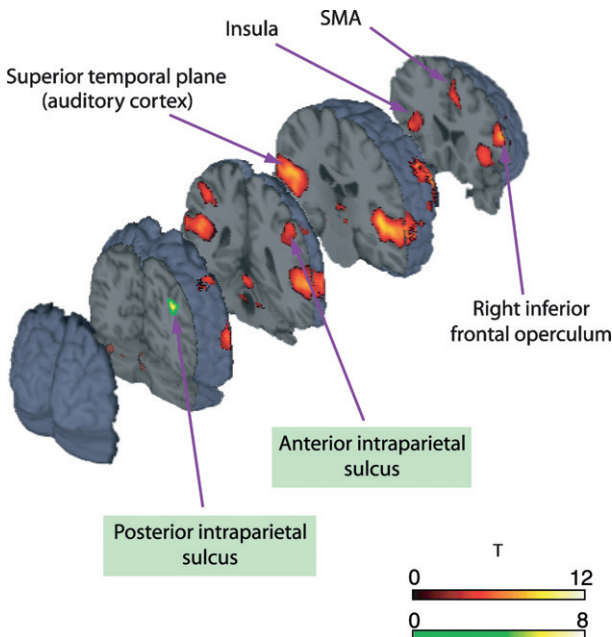


FIGURE 7.13 Cortical areas for auditory stream analysis: region (shown in light green) in the intraparietal sulcus (IPS) when two auditory streams are perceived versus one. The IPS has been implicated as a region for perceptual organization (binding) of multimodal (vision, touch, sound) information. Source: Adapted from Cusack, 2005.

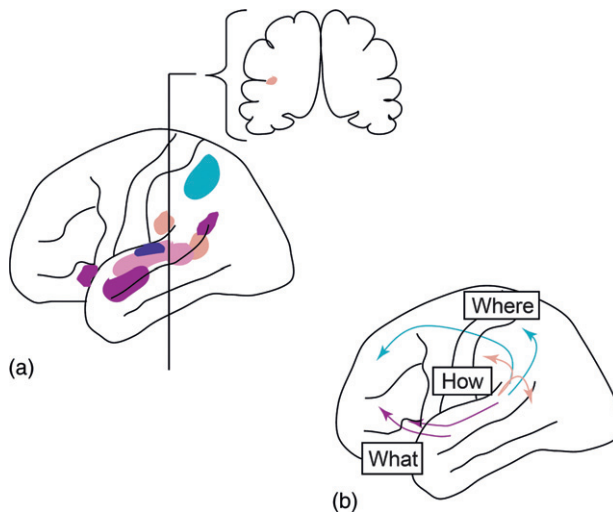


FIGURE 7.14 Functional responses to speech and candidate stream of processing in the human brain. (a) The lateral surface of the human brain: the colored regions indicate broadly to which type of acoustic signal each temporal region (and associated parietal and frontal region) responds. Regions in blue show a specific response to language-specific phonological structure. Regions in lilac respond to stimuli with the phonetic cues and features of speech, whereas those in purple respond to intelligible speech. Regions in pink respond to verbal short-term memory and articulatory representations of speech. Regions in green respond to auditory spatial tasks. (b) The putative directions of the “what,” “where,” and “how” streams of processing in the human brain. Source: *Adapted from Scott, 2005.*

4.0 SPEECH PERCEPTION

Now let’s turn to an important area of investigation in the topic of human auditory function: the decoding of speech sounds. The basic task of the speech system is to map sounds onto meaning. This seems to be a relatively straightforward process: when a speech sound, such as “d,” is heard, the physical sound is mapped onto an abstract representation of that sound: the *phoneme*. The two main types of phonemes are consonants (such as “d”) and vowels (such as “i”). Individual phonemes are stored in echoic memory while an entire word is being spoken—for example, “dig.” In order to decode the spoken word “dig,” you might imagine that the neural representations for “d,” “i,” and “g” are decoded individually and sequentially, and combined to map onto a sound representation of the word “dig.” The result is that the word “dig” is activated in the semantic/conceptual knowledge system. Unfortunately, this description makes perfect sense, but it is not how the speech system actually works. In fact, there is little agreement in the field of speech perception regarding the basic “building blocks” of speech. Is an individual phoneme the smallest unit of analysis for speech systems, or is the syllable the appropriate unit?

The speech system must not only decode the individual phonemes in speech to map the sound information to meaning, but it must also decode “who” information in order to know who is speaking and “when” in order to understand the temporal order of speech phonemes, syllables, words, and sentences. As mentioned earlier in the chapter, the speech signal must be evaluated across multiple time scales (20, 200, 2000 ms) (see [Figure 7.2](#)). This information must be decoded accurately regardless of the differences in human speech: whether we hear a high-pitched voice of a child or a low-pitched voice of a man, whether we are speaking very loudly or whispering, or whether we are speaking quickly or slowly. Obviously, the speech system is doing a lot more than a simple mapping of sound onto meaning, and it cannot rely

solely on the physical aspects of speech, since they vary so widely both within and across speakers. Despite the intricacies of speech perceptual processes, they occur with little attention or apparent effort on our part.

4.1 Early theories of speech perception

An important outcome of early speech science was the realization that the physical features in individual speech sounds or phonemes did not provide invariant information for their decoding (Figure 7.15). The findings of lack of invariance in speech sounds indicated that speech decoding systems must be quite different from those for decoding other types of sounds (see Box 7.1 to read about advances in this kind of sound decoding). One theory was that the neural systems for speech decoding were specialized and not part of the general auditory system. A strong view of this theory that “speech was special” held that the special systems for speech decoding occurred as early as the ear (Liberman et al., 1967). The lack of invariance finding led Liberman and colleagues to develop the *motor theory of speech perception* (for a review, see Liberman and Mattingly, 1985). This theory suggested that speech perception was tightly coupled to speech production, specifically the motor articulation processes or gestures used in producing speech. While the acoustics of phonemes lack invariance, the motor theory held that the articulatory gestures used to produce them were invariant and the neural representations of these gestures were accessed in speech perception. More recent theories, such as those proposed by Hickok and Poeppel (2004, 2007), have provided convincing evidence using fMRI studies that the motor theory as proposed does not hold up in light of modern neuroimaging data. Despite this evidence, the debate continues!

4.2 Functional mapping of speech-specific processes

Early neuroimaging studies by Binder and colleagues (for a review, see Binder, 1997) investigated stimulus-based differences in the auditory cortex by comparing brain activation in response to speech sounds (words) versus tones or noise. A general finding was more widespread activation in superior temporal gyrus and the superior temporal sulcus for words as compared to the tones or noise. Although these results could be interpreted as representing speech-specific processing in those auditory regions, they were difficult to

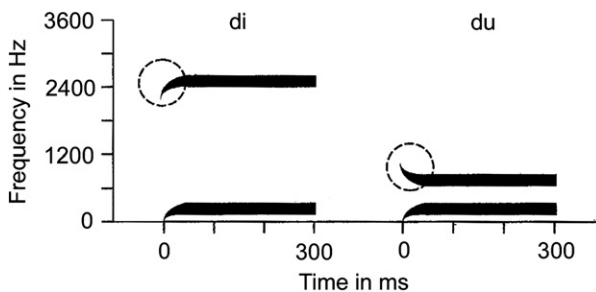


FIGURE 7.15 The direction and frequency of formant onsets in the syllables /di/ and /du/, demonstrating that, although the percepts of the two syllables beginning with the sound “d” will map onto a single phoneme /d/, the physical instantiations of the initial /d/ are quite different. Source: Carroll, 1999, originally from Liberman, 1970.

BOX 7.1

FROM VOCODER TO BIONIC HEARING

The technology underlying early vocoders remains in active use today and forms the basis for the way in which cochlear implants

stimulate the auditory system to provide hearing for individuals with certain kinds of hearing losses (see [Figure 7.16](#)).

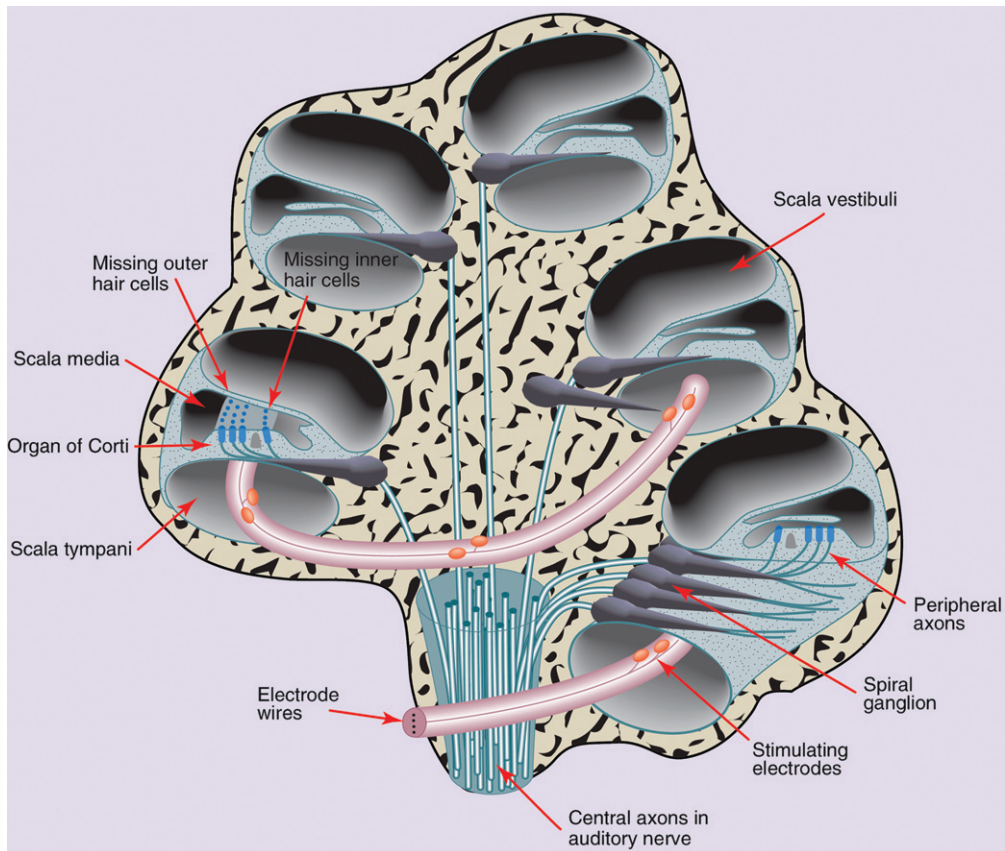


FIGURE 7.16 Cochlear implants stimulate the cochlea in the auditory system to provide hearing for individuals with certain kinds of hearing losses.

interpret, however, because words and the nonspeech sounds (tones, noise) differed not only in terms of representing speech versus nonspeech classes of sounds but also in their complexity. Therefore, different brain activation patterns might reflect speech versus nonspeech functional areas but might also reflect areas that differ in terms of decoding complex features in sounds.

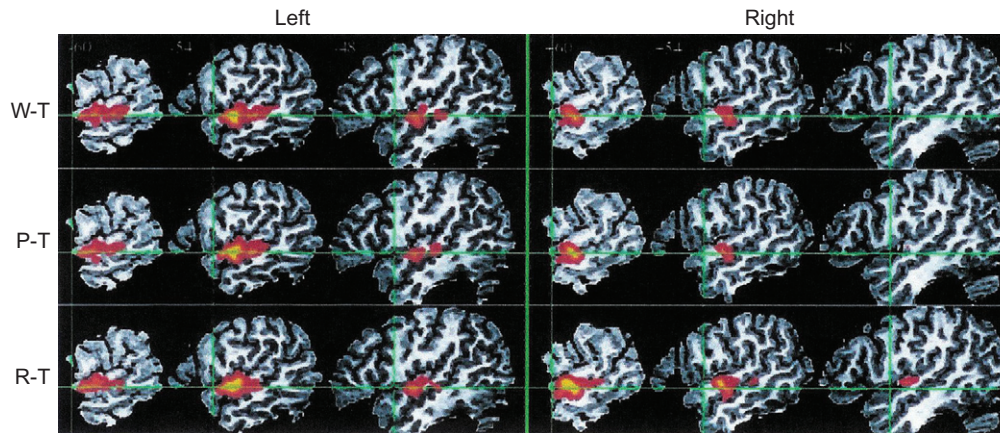


FIGURE 7.17 Comparison between three Speech-Tones contrasts (Word-Tones (W-T), Pseudowords-Tones (P-T), and Reversed-Tones (R-T)). Areas responding more to speech than to Tones are very similar for all contrasts. Source: Adapted from Binder et al., 2000.

A recent investigation addressed these issues with the presentation of many classes of sounds, including noise bursts, tones, words, pseudowords (pronounceable nonwords, such as “hig,” and reversed speech (Binder et al., 2000). The aims of this study were to investigate auditory cortical regions that were activated for speech versus nonspeech and compare regions that were activated for words versus pseudowords versus reversed speech (Figure 7.17).

The major findings were that Heschl’s gyrus and the planum temporale were activated similarly for all sound stimuli. This result supports the notion that sound is processed in a hierarchical fashion, with Heschl’s gyrus showing activation for all classes of sounds and likely representing an early sensory analysis. Speech sounds activated a larger region of the auditory cortex than the nonspeech sounds, extending into the posterior superior temporal gyrus and the superior temporal sulcus. Interestingly, the activation did not differ for words, pseudowords, and reversed speech. These findings indicate that speech activates a larger-scale network of the auditory cortex than the simpler noise bursts and tones. Because there were no differences between the words, pseudowords, and reserved speech conditions, Binder and colleagues concluded that these regions likely do not reflect semantic processing of the word meaning but reflect phonological processing of the speech sounds.

4.3 The link between speech perception and production

Early neuroimaging studies investigated brain activation for hearing versus producing speech. One important finding that has been reproduced many times is that the auditory cortex is activated during speech production tasks as well as during the perception of speech. Why is the auditory cortex active during speech production? Is it simply the case that while producing speech, we hear our own voice? Or does the auditory system play a role in speech production? There is evidence from neuroimaging studies, as well as from lesion studies with patients with aphasia, that speech perception and production systems are tightly coupled. From infancy, as speech and language are acquired, there are complex interactions between

heard language and spoken language that guide the development of language. In fact, Carl Wernicke proposed a model for language processing in the late nineteenth century that included a pathway from auditory speech perception areas to motor speech production areas and proposed that the “sound images” of words would serve to constrain the output when producing words. This model remains in use today, and while we know more about dynamic brain processes now than during Wernicke’s time, the model has provided an important theoretical framework for studying human language systems.

While there are clearly complex interactions between brain areas for decoding speech and producing speech, theorized in early motor theories of speech perception and realized in later brain studies, the exact nature of the integrative processes and neural territory that are shared during listening versus producing speech are still being elucidated in the field of human language research.

4.4 Damage to speech perceptual systems

Prior to the advent of neuroimaging, much of what we learned about brain systems for decoding speech came from investigations with individuals who had brain damage, typically due to a stroke, since they produce damage that is more limited in brain area than, for example, a closed-head injury. Strokes, nevertheless, can vary widely in the amount of brain area

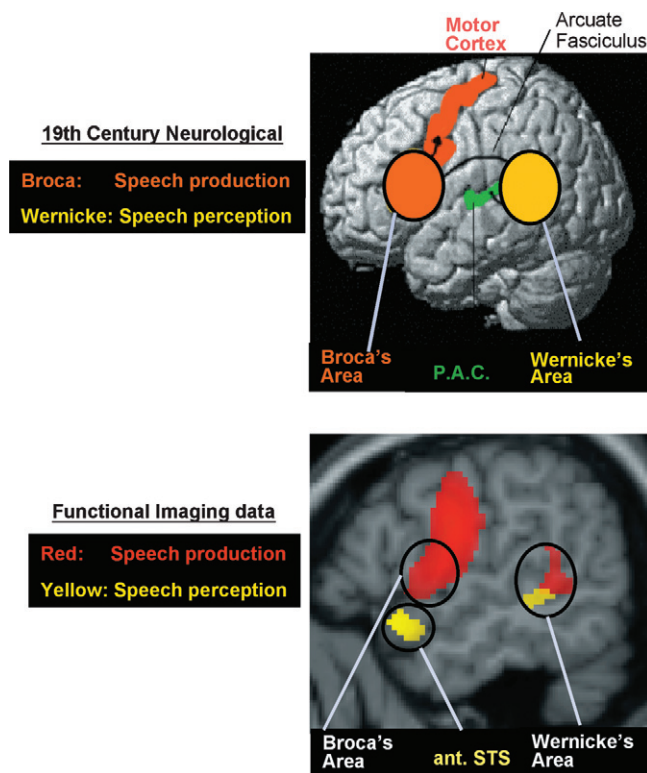


FIGURE 7.18 Orange and red shaded areas show activation for speech production, and yellow shaded areas show activation for listening to speech. (Note, green shaded area on the upper panel reflects localization of primary auditory cortex [P.A.C.]). Upper panel shows classical language areas adapted from nineteenth-century neuroanatomists. Lower panel shows contemporary view of the classical models. Source: Adapted from Frackowiak, 2004.

affected. The result of the stroke is a blockage of blood flow, which causes neuronal death and produces a lesion. The lesion in the area affected by the stroke, in turn, produces behavioral symptoms due to the brain damage. When a stroke patient has impaired language function, it is called *aphasia*. Patients with aphasia have widely varying symptoms depending on the location and the size of their lesion. Two basic classifications of aphasia come from nineteenth-century neuroanatomical investigations of brain areas for language: Paul Broca discovered a region in the inferior frontal lobe that was important for speech production, and Carl Wernicke discovered a region in the temporal lobe that was important for speech perception. Damage to these regions would produce aphasia with symptoms that differed depending on which area was affected. An individual whose major symptoms are impaired speech production is classified as a *Broca's aphasic*, and an individual whose major symptoms are impaired speech comprehension is classified as a *Wernicke's aphasic* (Figure 7.18).

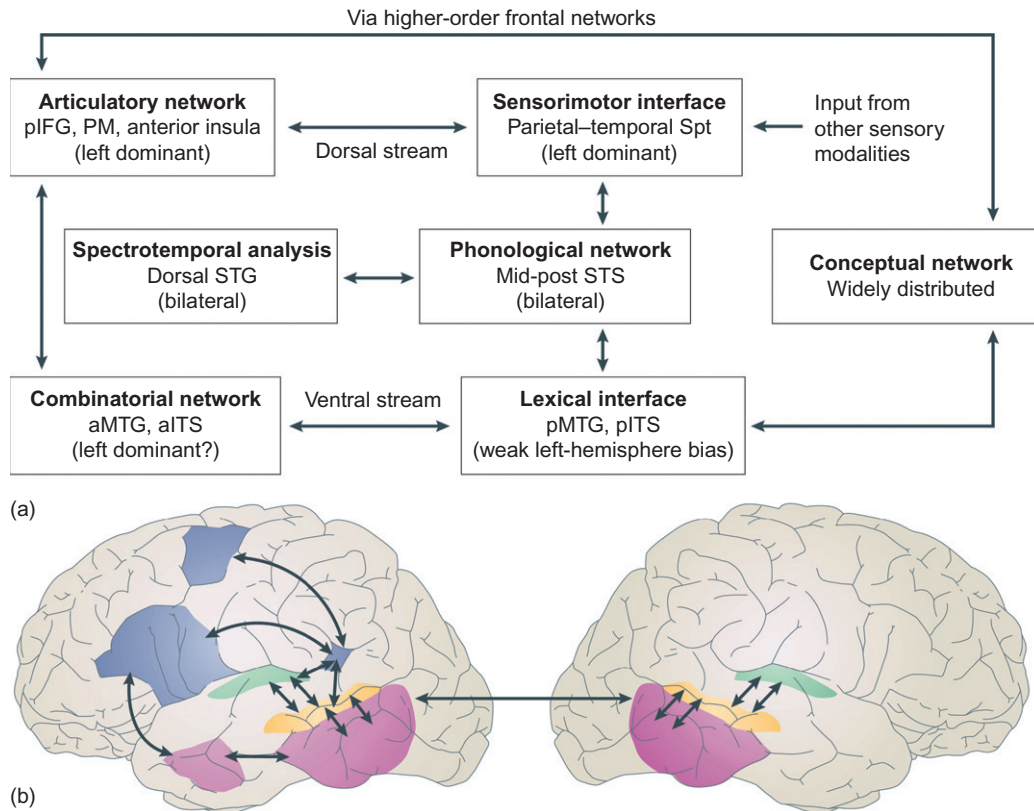


FIGURE 7.19 (a) Shows a schematic for the model of auditory language processing proposed by Hickok and Poeppel (2007). (b) Shows brain regions proposed to reflect stages of the model. Note that early speech perceptual systems (shown in green and yellow) for mapping the acoustic-phonetic information in sounds onto meaning are proposed to be mediated bilaterally in left and right hemispheres, while later processes are proposed to be mediated by left hemisphere regions. Source: Adapted from Hickok & Poeppel, 2007.

4.5 A working model for speech perception in the brain

For most right-handed individuals, language is lateralized to the left hemisphere. The language system is not unitary, however, and includes many computational stages, from decoding the speech sounds to form an abstract representation, to making contact with semantic and grammatical systems, to producing speech. A recent model of the auditory language system proposes that early speech decoding processes are organized bilaterally in the left and right auditory fields, while later semantic/syntactic processes are organized in the left hemisphere (Figure 7.19) (Hickok & Poeppel, 2007).

While we have learned a lot about how speech is processed in the brain through neuroimaging studies with healthy individuals and neuropsychological studies of individuals with brain damage, our understanding of how speech is perceived is still an ongoing investigation. Perhaps this is not surprising, since speech perception scientists have not agreed upon the basic units of analysis for speech perception! New techniques, such as TMS, and innovative experimental designs are providing new data for understanding how we decode speech and where in the brain these systems are located.

5.0 MUSIC PERCEPTION

Like speech perception, music perception is uniquely human. There are many similarities in speech and music perception: music has complex phrase structures, and its perception involves the mapping of sound onto meaning (and emotion). Music perception allows for the recognition of melodies despite differences in instruments, keys, and tempos; thus it cannot be a system built on absolutes but must have relative representations. Thus, music perception systems must have the ability to maintain a perceptual constancy in music representation. A central difference between speech and music perception is that all typically developing humans master speech perception. We are not only good at speech perception, but we are masters! This is not the case in music perception: there is tremendously more variability in music perception abilities and significantly more explicit learning that goes along with musical acuity. The variability in music perception abilities, combined with the many levels of musical training and skill, has made the study of music perception difficult because of these inherent individual differences. These difficulties, however, provide a unique opportunity in that they provide an opportunity to understand the effects of learning and plasticity in the brain areas that decode music.

5.1 Stages of music processing

The perception of features in music involves many stages of processing within the auditory system as well as across brain regions (Figure 7.20) (Zatorre et al., 2007). This processing must include both feedback and feedforward systems, as well as making contact with both stored memories and experiences, and emotional systems.

While the music signal is complex, like all sound, music has basic physical elements: frequency, intensity, and time. The psychological aspects of frequency and time in music correspond to pitch (melody) and temporal structure (rhythm). Traditionally, melodic and

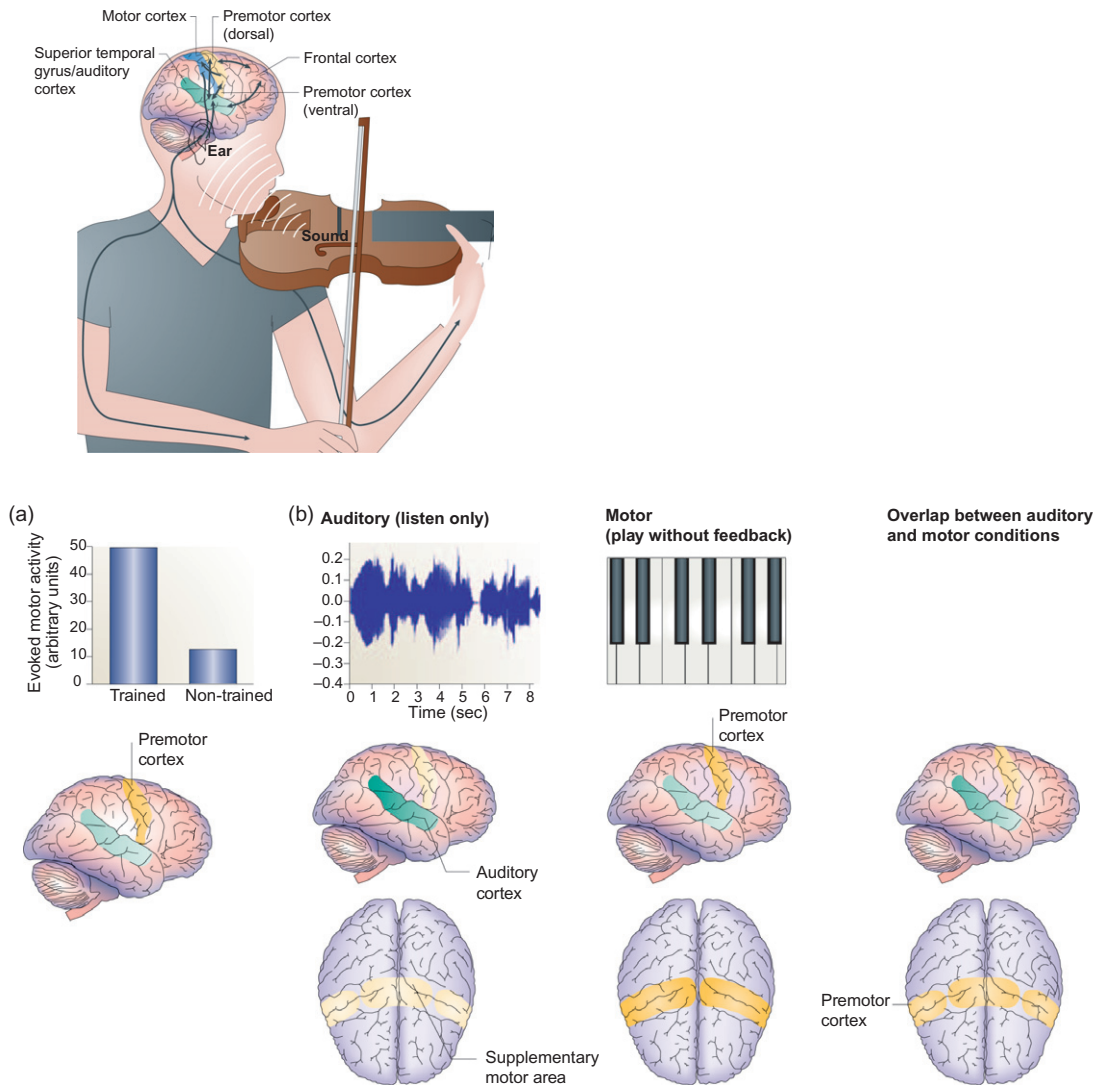


FIGURE 7.20 Top panel: Have you ever wondered what areas of your brain “light up” when you play or hear music? Of course, the auditory regions do activate when you play an instrument, for example, but so do many motor regions involved in the production of the sound from the instrument. In fact, these motor and sensory (auditory) systems are tightly coupled and together form a neural circuitry that provides feedback and feedforward information for musical instrument playing. Bottom panel: Results from several neuroimaging studies provide evidence for a tight coupling between activity in the auditory and premotor cortex. (a) People without musical training were taught to play a simple melody on a keyboard, and their brain activity for listening to that melody was compared in pretraining versus posttraining scans. Results showed activity in the auditory cortex, as expected, when listening to the melody, but there was also activity in the premotor cortex but only in the posttraining condition. (b) In other studies, researchers compared the brain activity of musicians while they listened to a piece they knew how to play (left column) with the brain activity while they played the same piece but without auditory feedback (middle column). There was significant overlap in the premotor cortex and in the auditory cortex, suggesting that the auditory and motor systems interact closely during both perception and production. Source: Zatorre *et al.*, 2007.

temporal aspects of music have been investigated as separate features of music perception. However, they likely are not completely independent. Just as some speech scientists propose that speech may be processed in brain areas specialized just for speech, music scientists have theorized that there may be neural systems specialized for music. Evidence in support of music-specific systems in the brain has been provided in neuropsychological studies with patients who have suffered brain damage. Peretz and colleagues provided a series of investigations with brain damaged individuals showing that, in some individuals, pitch or melody perception may be selectively damaged, leaving temporal structure perception intact, while in other individuals temporal perception may be damaged while pitch perception is intact. These findings have led to the development of a model for the brain organization for music perception (Peretz & Zatorre, 2005), where melodic features in music are processed preferentially in the right hemisphere and can be selectively impaired with right hemisphere brain damage, whereas temporal structure in music is decoded in a larger network of brain areas in both hemispheres.

5.2 A separate system for music perception?

Is music perception a separable aspect of auditory processing? While the work of Peretz and colleagues provides compelling evidence that this is the case, a recent review (Koelsch, 2005) of neuroimaging studies of music perception describes a growing body of evidence in support of the view that some aspects of music perception, notably the musical structure or syntax and the musical meaning or semantics, share neural territory with brain areas for language processing (Figure 7.21). The studies reviewed by Koelsch provide compelling evidence for at least some shared systems in music and language processing. Language and music are both uniquely human and highly structured signals, with multiple dimensions

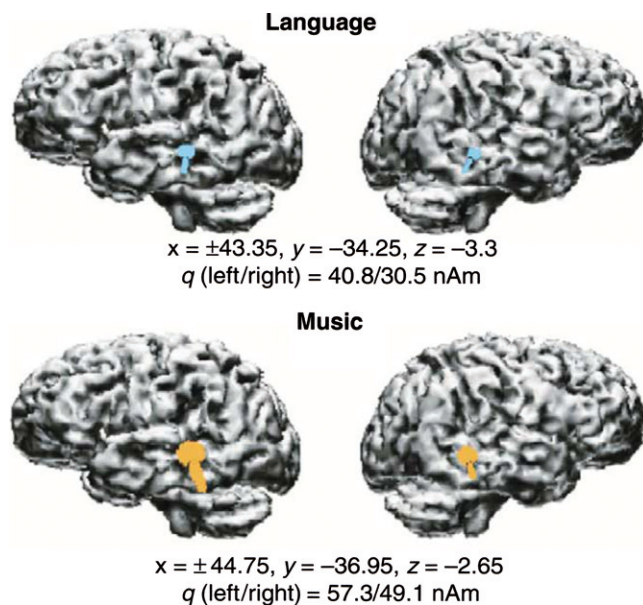


FIGURE 7.21 Top panel shows brain areas active for language. Bottom panel shows brain areas active for music. Source: Adapted from Koelsch, 2005.

along spectral and temporal axes for understanding their basic and complex structures. Perhaps there is no unitary brain region for either language or music: it may be the case that language and music systems have some neural territory that is specific for their processing and some neural territory that is shared.

6.0 LEARNING AND PLASTICITY

A central theme in the study of human cognition has been the investigation of how new information is encoded in the brain during *learning* and how the brain adapts and reorganizes to new situations or, following damage, *plasticity*. These issues are of theoretical value in understanding brain function but also have important practical relevance. One key question is how the auditory cortex responds to deprivation of sensory input due to acquired hearing loss, neural damage, or deafness. For example, if a child is born profoundly deaf and is fitted with a cochlear implant at age 2 (see Box 7.1), will his auditory cortex be receptive to sound and will he hear normally? Or will the two years of no exposure to sound limit the effectiveness of the implant? These and other questions regarding cortical plasticity are under intense investigation by auditory scientists.

6.1 Plasticity due to deprivation

Much of what we have learned about the plasticity of the auditory system due to deprivation comes from animal studies. In animal studies of neural plasticity after deprivation, specific areas in the cochlea or in the brainstem are lesioned so that a range of frequencies will no longer be encoded and transmitted to the auditory cortex. Following lesioning, the organization of the auditory cortex is studied to determine if there are frequency specific changes, reflecting neural plasticity. Irvine and colleagues conducted many studies using this general approach and reported evidence that the cortical frequency maps do indeed undergo changes following the lesioning (Rajan et al., 1993). We cannot ethically lesion human cochlea or brainstems, so our studies of plasticity following deprivation in humans must be accomplished in a noninvasive manner. While these studies are still in the early stages, there is evidence that adults with sudden onset high-frequency hearing loss have some changes in neural population response in the auditory cortex, implying that cortical organizational changes occur following hearing loss in humans in a manner similar to findings in animal studies (Dietrich et al., 2001). However, these adults had sudden onset hearing loss, and far less is known about slow onset hearing loss that may occur over many years or about more subtle forms of hearing loss.

What about children who are born with partial or complete deafness? When they are fitted with hearing aids or implanted with cochlear implants, will they develop normal hearing? Eggermont and colleagues investigated the responses in the auditory cortex in typically developing children and children with hearing loss who had cochlear implants (Ponton et al., 1996a, b). The implanted children showed some maturational lag compared to the controls. However, following implantation their auditory system continued to mature in a typical fashion, showing evidence for plasticity in the implanted children. These results are heartening in that they show that the auditory cortex may develop in a typical way even if there is deprivation early in life.

6.2 Plasticity due to learning

Our auditory system is constantly exposed to novel sensory inputs that must be decoded in order for us to interpret our listening environment. New voices, musical melodies, and environmental sounds are learned every day. What are the brain mechanisms for learning new sounds? How are these new sensory memories formed, and where are they located in the brain? These questions have been the topic of years of investigation by scientists using animal models for understanding learning and plasticity in the auditory system. While some scientists hold that sensory-based memories are formed and stored in central memory systems, others suggest that these sensory-specific memories are formed and stored within the sensory area in which they were learned. For example, Weinberger and colleagues (see Rutkowski & Weinberger, 2005, for a recent review) developed a model for auditory learning that holds that the changes in neural tuning for new and relevant sounds happen almost immediately, within a few trials of training, and occur in the primary auditory (A1) cortex. According to this view, the neural tuning of neurons in A1 changes to reflect the features in sounds that are behaviorally relevant.

6.3 Plasticity due to expertise

Noninvasive behavioral studies show similar patterns for learning in humans in that learning changes occur fairly rapidly and are relatively long lasting. One aspect of learning that has intrigued scientists is whether highly trained musicians have a different kind of brain than unskilled individuals. Certainly, the musicians have spent more time and effort on musical training, but does this change the way their auditory cortex is tuned? The work of Rupp and colleagues provides evidence that it does (Schneider et al., 2002).

7.0 AUDITORY AWARENESS AND IMAGERY

We can close our eyes and shut out visual images, but we cannot close our ears to shut out auditory events. What is the effect on the auditory system? The auditory system is the last sensory system to fall asleep (or become unconscious with sedation) and the first to awaken. In this section, we highlight some recent studies of auditory awareness during less-than-conscious states, such as sleep or sedation. We also highlight studies of auditory activation for imagined-not-heard sounds.

7.1 Auditory awareness during sleep and sedation

Think about the best way to wake up a sleepy friend: call his name! A neuroimaging study investigated brain responses in sleep and in wakefulness in two conditions: neutral, where the sound was a simple beep, and significant, where the sound was the subject's own name (Portas et al., 2000). Two main results of that study were that beeps and names activated the auditory cortex both when the subject was awake and when the subject was sleeping, indicating that the auditory cortex processes sounds even during sleep. A second key finding was that the auditory cortex response for the neutral tone versus the subject's name did not differ during sleep, indicating that auditory processing during sleep encodes the presence of sounds but did not differentiate between these very different sounds. Brain activation

patterns for names versus tones did differ, however, in middle temporal gyrus and frontal lobe regions. There were also areas in the amygdala that were more active during the presentation of the subject's own name during sleep than when awake. Do these brain areas represent a circuit in the brain that alerts us to wake us up when we hear our own name? More investigations are needed to support this theory, but these findings provide intriguing evidence for how the auditory system “wakes itself up.”

7.2 Auditory imagery

“Sounds not heard” are playing in our heads all day. Some sounds are uncalled for; they just seem to happen: a melody that spins around in your head, your inner voice talking to yourself. Other sounds that are not heard aloud are planned: practicing lines for a school play or rehearsing a phone number before dialing. Where are these sounds processed in the brain? We are aware that we actually seem to “hear” these inner sounds. Does that mean that the auditory cortex is activated when they are playing despite the fact that there is no actual sound? Zatorre and Halpern (2005) investigated this question using neuroimaging techniques to measure brain activation for imagined sounds versus heard sounds. Results (Figure 7.22) show that the nonprimary auditory cortex is indeed active during imagined—and not heard—sounds.

A related finding was reported by Jancke and colleagues (Bunzeck et al., 2005). These investigators wanted to study auditory imagery for environmental sounds. Using fMRI, they recorded neural responses to subjects perceiving sounds and imagining those sounds. Results are presented in Figure 7.23: the primary and secondary auditory cortexes in both hemispheres are active when perceiving sounds (left panel), while the secondary (and not primary) auditory cortex is active when imagining those same sounds (right panel). These findings provide compelling evidence that imagined sounds activate similar neural regions in the auditory cortex that are activated when sounds are heard. The findings presented here, while representing only a small proportion of the ongoing investigation of auditory imagery, indicate that similar processes occur in humans as well, with imagining and perceiving sounds sharing neural territory.

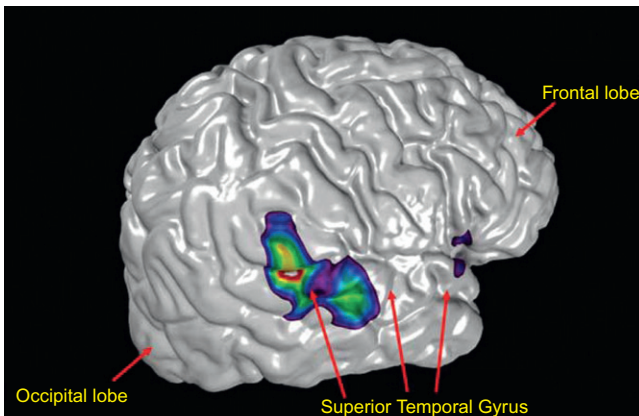


FIGURE 7.22 Brain areas active for imagined sounds. Source: Adapted from Zatorre and Halpern, 2005.

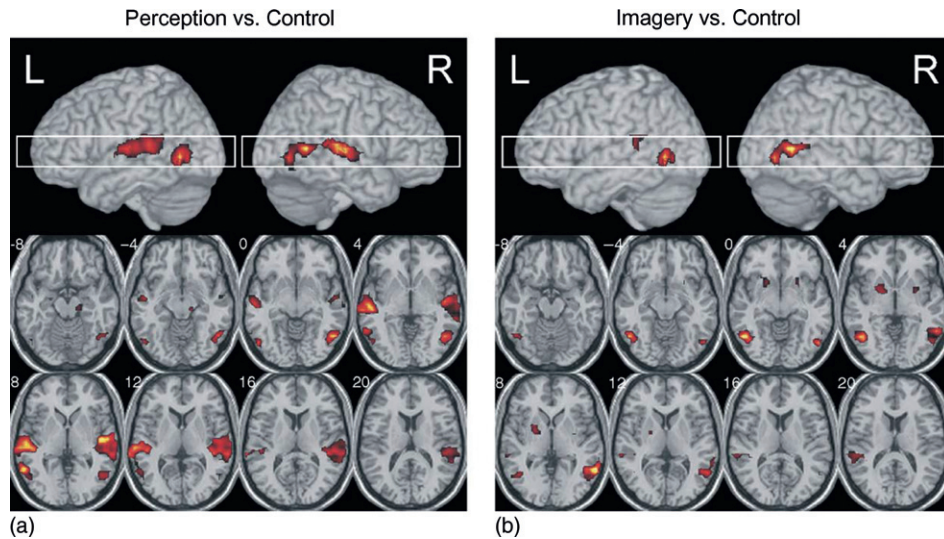


FIGURE 7.23 fMRI study of perceived sounds versus imagined sounds. The sounds used in this study were neither language nor music, in order to determine the localization of imagined nonlinguistic or musical sounds. The primary auditory cortex was active during the perception phase (a) of the experiment but not during the imagery phase (b). Source: Adapted from Bunzeck et al., 2005.

8.0 SUMMARY

In this chapter, we presented an overview of the complex auditory system, from hearing basics to music perception to auditory imagery. The advent of neuroimaging techniques has provided a wealth of new data for understanding the cortical auditory system and how it interfaces with other cortical regions. While we have made major inroads on understanding the puzzle of auditory perception, there is still much work to be done. For example, teasing apart neural systems that underlie music and speech perception is still in the early phases. There are many other key questions that are being addressed in the field of auditory brain science. For example, what are the differing roles of the left and right hemispheres in speech and music perception?

There is fruitful work in the investigations of processing streams in the auditory system and in the brain. And while the work in nonhuman primates has informed us greatly about the existence of “where” and “what” processing streams, these streams may be established differently for humans due to the unique and important roles of speech and music perception in the evolution and development of the human brain. The next time an uncalled melody plays inside your head, consider the areas that might be activated in your brain as you “hear” your silent song!

9.0 STUDY QUESTIONS AND DRAWING EXERCISES

9.1 Study questions

1. What are the basic physical features and psychological aspects of sound?
2. What are the main parts of the auditory system and what are their roles in perception?
3. Briefly describe some differences between the “what” and “where” processing streams.

4. What are the basic units of analysis for speech perception?
5. What have new brain imaging techniques provided us in terms of investigating auditory function?

9.2 Drawing exercises

We highly recommend drawing and coloring to help you remember the physical layout of the brain.

1. Top panel of [Figure 7.24](#): identify the auditory cortical areas that are visible on the lateral aspect of the brain.
2. Bottom panel of [Figure 7.24](#): identify the auditory cortical regions denoted by blue, pink, and brown shading.

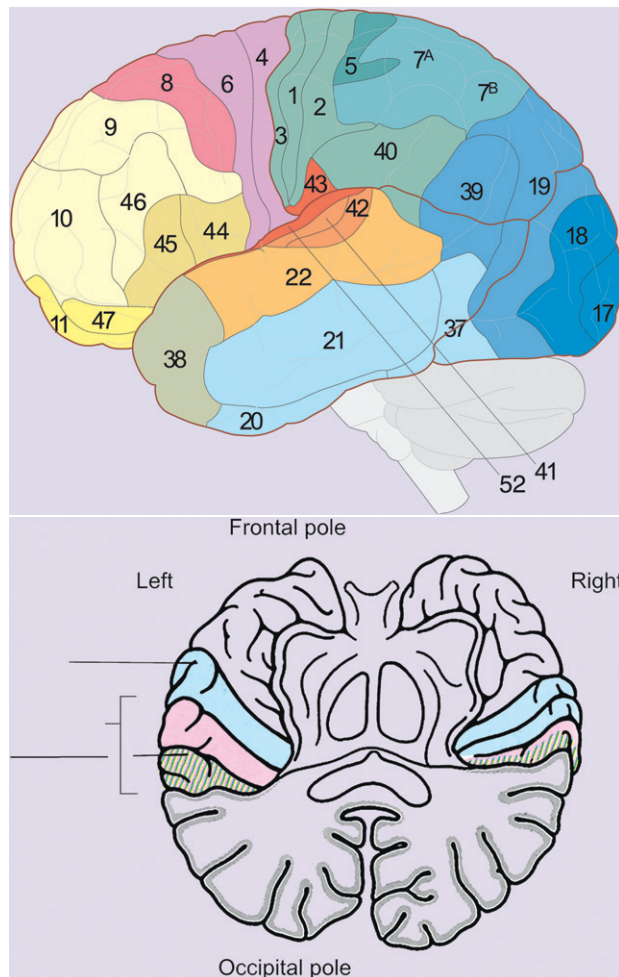


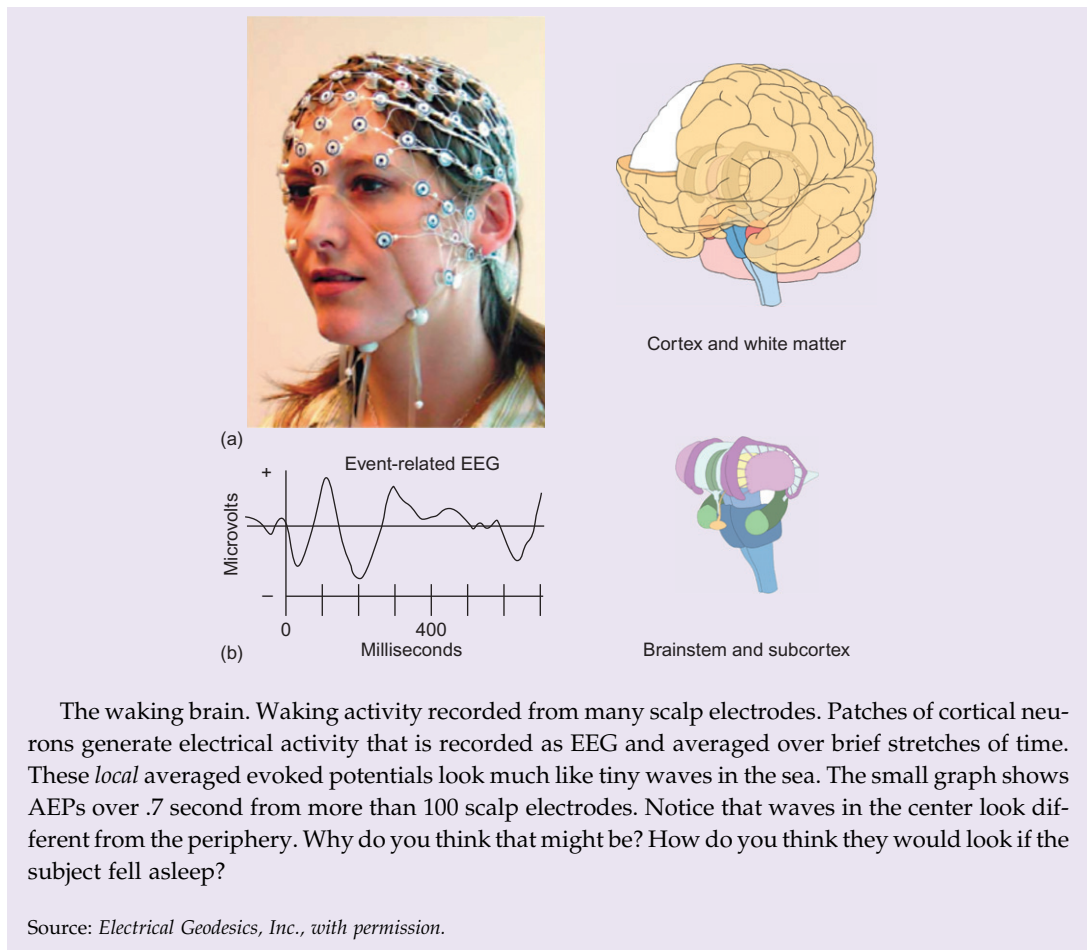
FIGURE 7.24 An axial (horizontal) slice of the brain showing the anatomy of the auditory cortex in the left and right hemispheres.

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The brain is conscious

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1.0 INTRODUCTION

Consciousness is the water in which we swim. Like fish in the ocean, we can't jump out to see how it looks from the outside. As soon as we lose consciousness, we can no longer see anything. Ancient people knew about waking, sleep, and dreaming because they experienced those states in themselves, and they could see other people when they were sleeping and waking. Sometimes clan members would wake up from a dream and tell others about their inner journeys. All human cultures know about the three basic states.

Scientists also *combine objective evidence with subjective reports*. Scientific studies usually have ways to double-check the reports people give about their experiences. For example, we know that REM dreams show an unmistakable pattern of activity: The EEG shows low voltage, fast, and irregular waves, and the eyes move back and forth in fairly slow and large movements.

When we awaken people during REM dreams, they tend to tell us about vivid, dramatic but frequently disrupted experiences. Whenever we find both the objective signs of REM dreaming and subjective reports from people awoken during those periods, we can feel confident that we have converging evidence that people are telling us about “real” dreams.

1.1 Three global brain states

Sleep, waking, and dreaming are easy to identify based on our own experiences—and also by the electrical activity all over the brain. Steriade (1997), a leading scientist in this field, wrote, “The cerebral cortex and thalamus constitute a unified oscillatory machine displaying different spontaneous rhythms that are dependent on the behavioral state of vigilance.” We will take Steriade’s one-sentence summary as the theme of this chapter. As we will see, the cortex and thalamus work very much like an oscillatory medium, like the ocean. In addition, we know from earlier chapters that the cortex consists of flat arrays of neurons. Indeed, we can think of the cortex and its related brain regions as a huge, oscillatory array of many hundreds of arrays.

For many years the underlying mechanisms for these electrical patterns were unknown. There was debate about whether EEG was even a useful measure. However, basic research has now shown that scalp EEG reflects the fundamental “engine” of the thalamus and cortex. Although the brain’s electrical field is only a side effect of the normal working of the core brain, we can use EEG to understand how the thalamus and cortex do their work.

Figure 8.1 shows the three daily states recorded from one electrode on the scalp. One electrode is enough because states of consciousness involve *global* activities, like day and night traffic in a large city. If daytime traffic is very heavy and nighttime traffic is very light, only one observation point can show the difference.

The daily (circadian) cycle is controlled by precise biological mechanisms, stimulated by daylight and darkness, and by eating, activity patterns, sleep habits, and other factors. A small group of receptors in the retina detect daylight and darkness, signaling the suprachiasmatic (SCN) nucleus, the pineal gland, hypothalamus, and deep brain nuclei to release state-specific chemicals called neuromodulators. Melatonin is an important sleep hormone triggered by the onset of darkness.

Chemical neuromodulators spread very widely in the brain and help to trigger global states (Figures 8.2 and 8.3).

Keep in mind that the thalamus is the “gateway to the cortex.” Most thalamic nuclei are constantly signaling back and forth to corresponding parts of the cortex. The thalamus and the cortex are often considered to be one large functional “engine.” When we shift between major circadian states, the engine changes gear.

Figure 8.4 shows the neural control circuit of the thalamus and cortex, consisting of three connected cells in cortex, thalamus, and the reticular nucleus of the thalamus. The upper neuron in Figure 8.4 is a pyramidal cell in the cortex. Together this circuit works as a “pacemaker” for the major states of the circadian cycle. Signaled by neurochemicals from the brainstem, the three-neuron circuit “pumps” the giant cortico-thalamic core. There are millions of such circuits, but the simplicity of this loop is striking. Notice that the circuit is itself triggered by chemical neuromodulation from the brainstem.

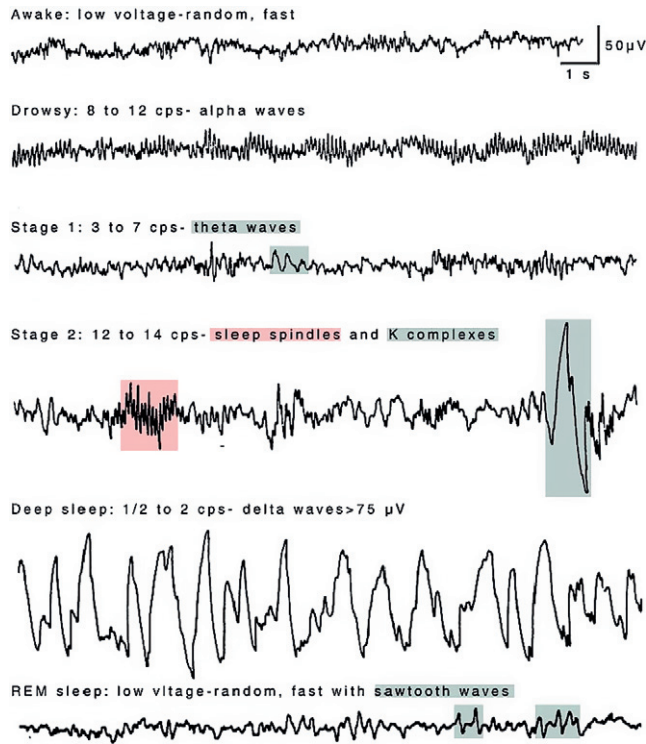


FIGURE 8.1 EEG of waking, dreaming, and deep sleep. To identify brain states, we only need one electrode on the scalp (and a reference electrode that is often attached to the ear). Global states can be identified just by looking at EEG. Waking consciousness and REM dreaming look remarkably similar, consistent with the fact that we experience a rich flow of conscious events during both waking and dreams. Deep sleep looks very different: it is high in voltage, slow, and regular. Source: *Squire, et al. 2008.*

2.0 WAKING: PURPOSEFUL THOUGHTS AND ACTIONS

Waking is our time to open up to the world around us, perceive and explore, think about ourselves and one another, learn and prepare for the future, cope with challenges, express our emotions, and advance our personal and social goals. From a biological point of view, all of our *purposeful* survival and reproductive activities take place during the conscious state.

We have used a “functional diagram” of human cognition since [Chapter 2](#). What we haven’t said is that the waking state is *the necessary condition* for all those mental functions. That fact has many surprising consequences for our understanding of the brain. For example, the global features of the conscious state ([Figures 8.1–8.4](#)) may not be obvious, but we know they are necessary for us to have conscious sensations, working memory, and voluntary control of our muscles.

It will help to take another look at our basic functional diagram ([Figure 8.5](#)) and think about the boxes that work only in the waking state. They are generally the colorful ones. The gray boxes (long-term memories) continue to store information 24 hours per day. As we will see, conscious experiences we learn during waking periods are often consolidated in slow wave sleep.

Sensory consciousness obviously also depends on the waking state, as do the “inner senses” of verbal rehearsal (inner speech), the visuospatial sketchpad (imagery), and the like. Normal, voluntary control is mainly limited to the waking state.

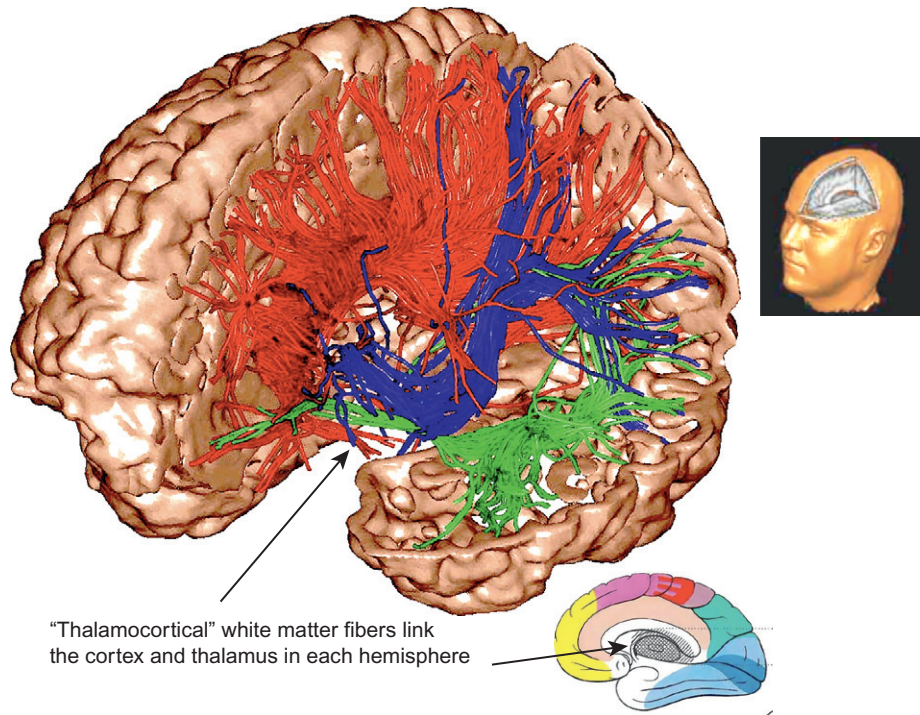


FIGURE 8.2 The cortex and thalamus make up one unified system. The massive size of axonal fiber tracts between the thalamus and the outer layers of cortex. Since axons coming from each cell body are wrapped in glial cells that are filled with lipid molecules, they appear white to the naked eye and therefore were called the “white matter” by traditional anatomists. These tracts are artificially colored in this computer-generated graphic to show the different major pathways. All the fiber tracts seem to emerge from the left thalamus from the point of view that is shown here, but at least equal numbers of axons travel from cell bodies in cortex to the corresponding nucleus of the left thalamus. Traffic is always two-way or “reentrant” in the thalamocortical system, a fundamental fact that requires explanation. Notice that there is no cross-hemisphere traffic in this image. The next figure shows equally massive cortico-cortical highways connecting the hemispheres laterally, mostly flowing across the corpus callosum. As [Chapter 3](#) points out, it is possible to lose an entire hemisphere without losing consciousness as long as the second hemisphere is spared along with the brainstem. Source: *Izhikevich & Edelman, 2008*.

Voluntary selective attention also occurs primarily during waking. Voluntary attention is shown in [Figure 8.5](#) as an arrow running from the central executive (roughly, the frontal lobes) to brain activities that are enhanced by attention. Spontaneous attention is not under voluntary control, but if someone yells out loud, a large dog barks unexpectedly from a few feet away, or a truck looms into your field of vision, attention will be “stimulus-driven.”

Many biologically significant events trigger attention “bottom up,” such as the smell of food when you are hungry. We spontaneously pay attention to personally significant stimuli as well, like the sounds of our own names. In the figure we symbolize stimulus-driven attention with an arrow coming from the sensory boxes of the diagram to suggest that some stimuli are inherently attention-capturing.

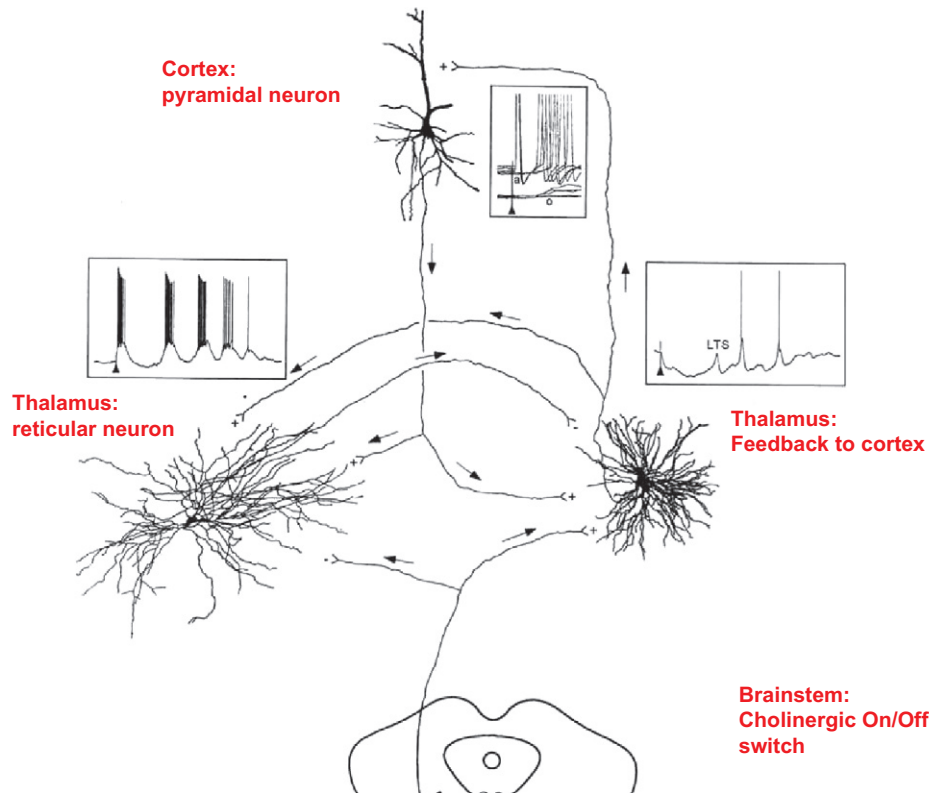


FIGURE 8.3 The state control circuit: three neurons in a thalamocortical loop. The basic rhythmic “pump” of the brain. Waking, sleep, and dreaming are driven by thalamocortical oscillations. Thalamic nuclei interact closely with corresponding regions of cortex. This core brain is shared by other mammals and birds. Source: *Adapted from Steriade, 2006.*

Later in this chapter we will see that dreaming has some features of waking consciousness, such as vivid conscious imagery and working memory. Still, the fact remains that our goal-directed actions happen during the waking state, including thinking and problem solving, food gathering, social behavior and mate seeking. It makes sense therefore that task-related signaling in the brain is mostly found in waking consciousness.

2.1 The stadium analogy: chattering, cheering, and chanting

Waking EEG has puzzled scientists since 1929, since it looks very irregular, even random, as if it's a kind of “white noise,” such as the random noise we hear from waterfalls and ocean waves. If we record the sound of a waterfall and then average separate stretches of sound, the average will look like a flat line with zero voltage. That is because random activity is so unpredictable that it adds up to zero. The chance of a voltage at any moment being above and below zero is about equal. As we've seen with the averaged evoked potential in [Chapter 5](#), we can

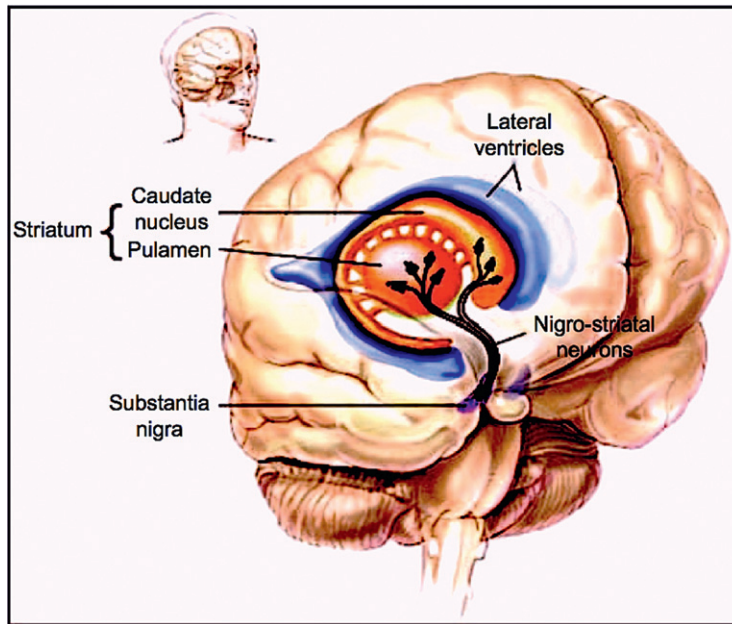


FIGURE 8.4 Chemical switching controls the state circuit. The daily states of consciousness are turned on and off by surprisingly small numbers of neurons, located at the bottom of the brain in nuclei like the substantia nigra (SN), as in the figure (dark substance). Their widespread axons spray special neurochemicals called “neuromodulators” to modify local neurotransmitters. The bundle of axons that project from the small SN in the bottom of the brain are called the nigro-striatal neurons because they start at the substantia nigra and terminate in the striatum (“striped region”) of the basal ganglia. Source: U.S. National Institute of General Medicine.

use that fact to obtain beautiful AEP curves that are time-locked to a stimulus. The random EEG just drops out of the averaging process.

2.1.1 Chattering in the waking brain

If we think of the brain as a huge football stadium with thousands of people just chattering with one another, the averaged sound is so irregular that it resembles white noise. However, every conversation in the stadium is very meaningful to the people doing the talking. We see *local synchrony* between two individuals in a conversation and *global randomness* because none of the conversations are linked to one another. It’s convenient to call this the “chattering” state of the football stadium.

Figure 8.6 shows that during the waking state, neurons in different parts of the cortex and hippocampus are “phase-locked” to one another. (Phase-locked simply means “synchronized with a small lag time.”)

The evidence comes from Cantero and colleagues (2005), who recorded from hundreds of neurons directly in the brain of an epileptic patient. Notice that the “Waking” column shows very high correlated activity between different parts of the cortex (top) and also between the hippocampus and neocortex. Both of those regions are very active during waking, but we now know that they are also highly correlated with each other at the single neuron level. That is analogous to spectators in the stadium talking “in sync” with one another. But like the

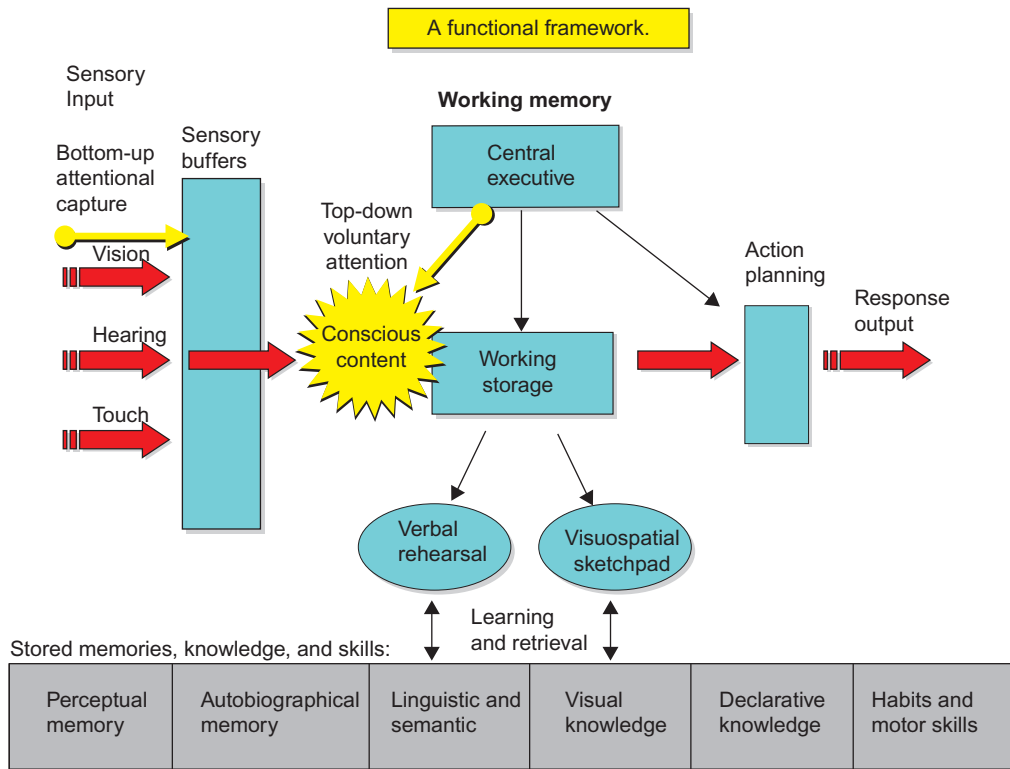


FIGURE 8.5 We are *not* conscious of all cognitive functions at the same time, but we can get rapid conscious access to all the *colored* boxes in the diagram. The *gray* boxes at the bottom are never directly conscious. However, we can *retrieve* conscious information from long-term memories. Notice that the diagram looks very different in dreams and sleep. Source: Baars, with permission.

chattering people in the stadium, their conversations are independent of one another. If we record the overall sound in the stadium, it seems random, but if we record the talk of two people in a conversation, we can see the synchronized activity.

Although the stadium analogy is not supposed to be taken literally, two people talking to each other do “dance” in synchrony with each other, so a slowed-down video of a conversation will show them “micro-dancing” with each other. We can think of Figure 8.6 as showing relatively localized synchrony between regions of the brain that are working together. During deep sleep and dreaming, that kind of synchrony breaks down, as you can see in the second and third column of the figure.

The conscious state therefore seems to support local synchrony (or phase-locking), while deep sleep and dreaming do not. As we will see next, there is very direct evidence that synchrony serves as an important coordinating rhythm for neurons that may be widely dispersed but that are supporting the same cognitive task, whether it is sensory perception, motor control, memory storage, or the other active tasks in our functional diagram (see Figure 8.5).

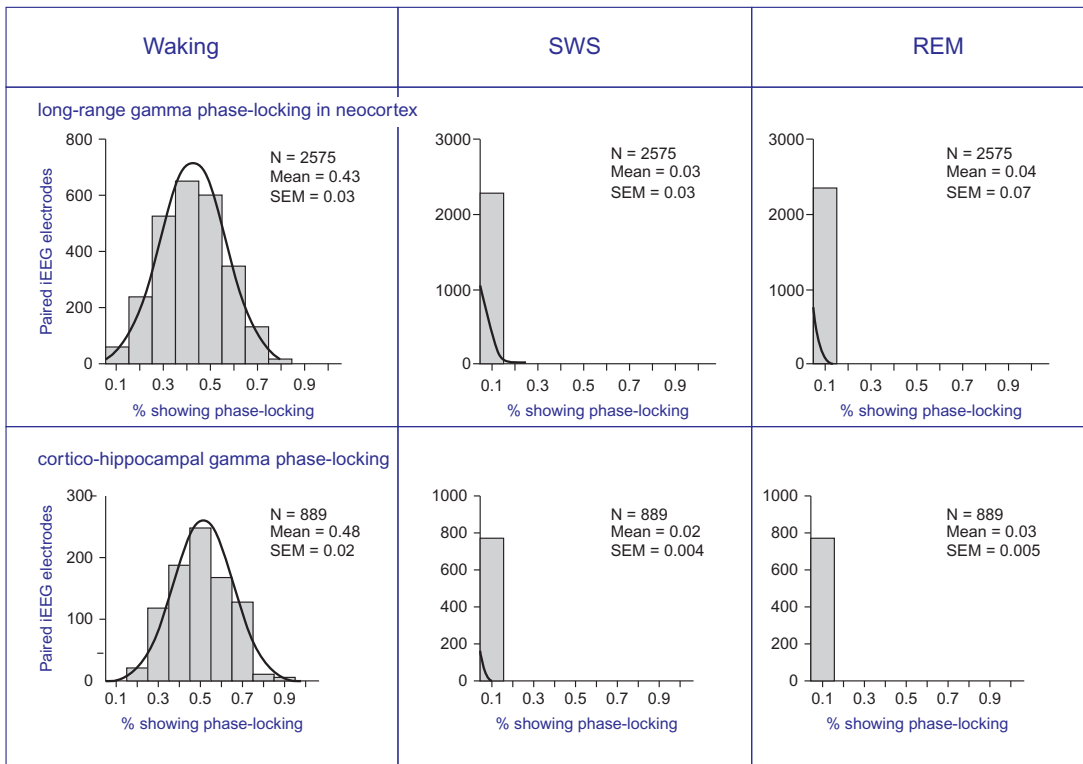


FIGURE 8.6 Synchronized “conversations” between neurons during waking. If we think of each neuron as a spectator in a large football arena, during the conscious state thousands of spectators are chattering with one another at the same time. Each dialogue synchronizes just two people, but hundreds of different conversations are happening at the same time. There is *local* synchrony but not *global* synchrony. Source: Cantero & Atienza, 2005.

2.1.2 Cheering in the waking brain

Football spectators are not always chattering to one another locally. They do at least two massively coordinated actions. One we will call *cheering*, such as when one team scores a thrilling goal. Ten thousand people suddenly applaud (or boo) out loud. Since this is an event-related cheer, it is analogous to the event-related potential. In the brain we commonly average evoked potentials over a number of triggering events, like the thrilling football play that triggers a cheer. That is the averaged evoked potential. Sending a big flash or a loud noise through the brain is very much like a simultaneous cheer going through a football stadium. Suddenly all the noisy background chat turns into a giant “hooray!”

2.1.3 Chanting in the unconscious brain

What about unconscious periods, like deep sleep (slow wave sleep)? You can see in [Figure 8.1](#) that it consists of very large, very slow (by brain standards), and very coordinated brain activity. We know that billions of neurons are highly coordinated during SWS because

all their activity adds up during the UP state (the peak of the slow wave), and nothing seems to be happening during the DOWN swing of the slow wave.

In fact, direct brain recordings show that during the DOWN swing of the global wave most neurons in the cortex are pausing, while during the UP phase billions of neurons are firing. This is called “buzz-pause” activity, and it appears to be controlled by the neurons shown in [Figure 8.3](#): the state control circuit. Notice that some of these neurons are located in the thalamus and others in the cortex. (The whole circuit is also controlled by small clumps of neurons in the bottom of the brain, as shown in [Figure 8.4](#).)

The stadium analogy holds nicely for slow wave sleep, where billions of nerve cells are going “buzz-pause” over and over again, from 0.5 to 3.5 Hz ([Figure 8.7](#)). That is presumably why waking cognitive functions are largely lost during slow wave sleep.

We can get some confirmation of this hypothesis from the case of epilepsy. There are many different varieties of epilepsy, and not all involve a total loss of consciousness. But we can study cases that do lead to a temporary sleeplike state. [Figure 8.8](#) shows the EEG of a child with epilepsy. Childhood epilepsy is usually a passing condition but one that must be treated medically.

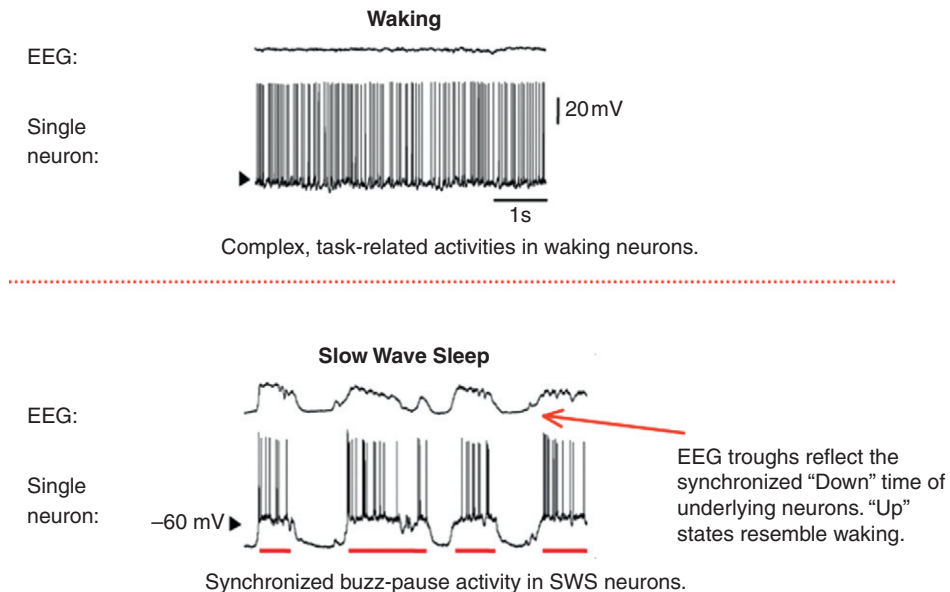


FIGURE 8.7 Chattering and chanting neurons. The waking EEG looks small, irregular, and faster than slow wave sleep. It is believed that waking (and REM dreaming) therefore involves more differentiated information processing in much the same way that a stadium full of talking people serves to process more information than the same people all chanting in unison. The unison chanting is largely redundant (you can predict the crowd chants from just one person) so the information content is lower. Because the chanting brain stops working from 0.5 to 3.5 times per second, we cannot do any cognitive work during the DOWN swings of the slow waves. Neurons can fire and even synchronize during the UP phase, but any task longer than a fraction of a second will be disrupted. You can think of it as rapidly switching a computer on and off, several times a second. The computer might be working when you turn it on, but by switching back and forth, you disrupt any long-lasting computational processes. Source: Adapted from Steriade, 2006.

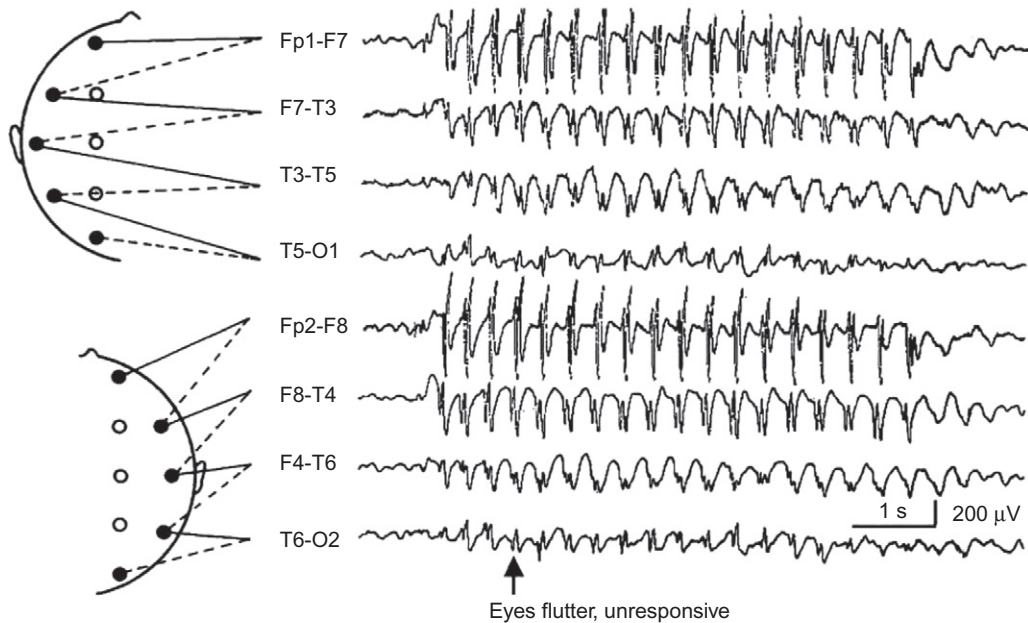


FIGURE 8.8 Slow hypersynchrony in epileptic loss of consciousness. The surface EEG of a 7-year-old girl during an epileptic seizure with loss of consciousness. Epileptic loss of consciousness shows slow, hypersynchronized global EEG similar to deep sleep but characteristically more jagged. Other unconscious states, like coma and general anesthesia, also show slow, high-voltage, and synchronized waves spreading over the cortex, suggesting that synchrony by itself is not the marker of consciousness. Tonic-clonic seizures are cortical. Source: *Blenkfled, 2005*.

Other unconscious states also show slow EEG waves, except for deep coma, which may show a very low voltage level so that peak waves simply drop out. However, scalp EEG sometimes fails to pick up EEG activity deep in the brain, so a low overall level of the EEG does not necessarily mean there is no consciousness at all. It is important to remember that scalp EEG only picks up 0.1 percent of the voltage level at the cortex. It is therefore possible to miss brain activity if we only look at scalp EEG.

In some cases, patients have been wrongly diagnosed as being in an irreversible coma when closer observations showed signs of consciousness (Laureys et al., 2002). Medical scientists have therefore proposed a new diagnosis called the *minimally conscious state* (MCS) for conditions that may look like coma on the outside but that may actually involve patients who have conscious periods.

2.2 How does the chattering brain do its work?

If the stadium analogy is right, most cognitive tasks happen during chattering states. That includes both waking and dreaming (see [Figure 8.1](#)). Waking and dreaming EEGs look irregular and low in voltage because there is no global synchrony. However, we expect there to be local synchrony (technically, local phase-locking).

We will discuss dreaming later in this chapter. Here we will only deal with the conscious waking state. The question is, how does a brain full of randomly chattering neurons do its work? After all, the waking brain does all the purposeful work we need to survive and propagate the species. The answer is now clear. In the giant stadium of the brain there are many *synchronized* conversations taking place between neurons “talking to” one another to get things done. There is nothing to evoke a global cheer in the stadium.

If we then compare the same patient during deep sleep and dreaming, there is no significant correlation between the same neurons. This evidence is what we would expect on the stadium analogy. Waking EEG is so irregular that different periods sum up to zero. The same thing would happen if we recorded random conversations in a football stadium. “White noise” is the technical word for random sounds, like the sound of a waterfall or a buzz of talking in a large auditorium.

What seems to be happening in conscious states is that the overall activity looks random, but all kinds of purposeful tasks are going on using local synchrony.¹ In dreams, much the same irregular EEG can be observed, except that we cannot perform survival tasks. The function of dreaming is therefore still unclear. We know, however, that executive brain functions are strongly inhibited and that sensory input is generally blocked as well. (Voluntary attention is not possible during sleep and only rarely during dreams.)

Deep sleep shows global synchrony (see [Figure 8.1](#)). In “slow wave sleep” (SWS), massive numbers of neurons show broadly synchronized *bursts* and *pauses* one to four times per second, adding up to slow, high-amplitude EEG waves. This is the least conscious state of the daily cycle, as measured by the arousal threshold—by playing louder and louder sounds until the subject wakes up.

The stadium analogy for deep sleep is tens of thousands of people chanting in unison. The total sound in the stadium therefore goes up and down in slow synchrony. Notice that because everybody is chanting the same words, the information flow inside the stadium is small. If everyone were carrying on separate conversations, much more information would be transmitted between people. SWS therefore looks like a state of *high redundancy* and *low information flow*.

In summary, in SWS billions of neurons “buzz” together and “pause” together. Waking shows much more differentiated and task-specific signaling. The difference between sleep and waking is not just behavioral and subjective, but it’s also in our ability to execute life-relevant tasks. The functional role of the conscious waking state has now clarified. Slow wave sleep has at least one known function, as we will see. However, we still do not know why we dream, though many ideas have been offered. Biological adaptations often have multiple functions. Our lungs are necessary for taking in oxygen and expelling CO₂, but they are also used to control speech, singing, shouting, whispering, and playing the flute. Lungs evolved when vertebrates began to populate the land, while human speech built on that ancient biological foundation only about 100,000 years ago.

¹ For example, the lower ventral stream of vision yields reportable conscious object representations, like visual coffee cups or a kitchen chair. The upper dorsal stream of the visual brain represents body space and controls actions like manual reaching, but its contents are not reportable as conscious (Milner & Goodale, 2008). Yet both the dorsal and ventral streams require the state of waking consciousness to work.

In the same way, the brain's circadian states are likely to have more than one function. The onsets of both waking and sleep trigger gene expression in hundreds of different neural genes. In waking we have easy access to a vast repertoire of skills and capacities. One of these is voluntary attention; we can decide to pay attention to this book or to yesterday's notes. Consciousness and attention are intimately related but are not identical. When we selectively attend to one thing over another, we become conscious of the attended object. Those conscious moments may then trigger further attentional selection, and so on. We cycle between experiencing things (consciousness) and deciding what we want to experience next (selective attention).

Figure 8.2 is a reminder of waking state functions, including selective attention. With 100 billion neurons firing about ten times per second, and excitatory neurons triggering off other excitatory neurons, you can imagine what an ocean of mutually pushing waves and troughs we have oscillating in our brains every second. Fortunately, most excitatory neurons are controlled by inhibitory neurons so the brain can regulate its state of excitation. Otherwise we might get epileptic seizures, with giant waves of excitation constantly triggering new waves so the cortex goes into overdrive. Like all the organs of your body, the activity of the brain is under careful homeostatic control.

TABLE 8.1 Major Features of the Conscious State

-
1. A very wide range of conscious contents
 2. Widespread brain effects beyond the specific contents of consciousness
 3. Informative conscious contents
 4. Rapid adaptation (learning and coping)
 5. The "fleeting present" of a few seconds
 6. Internal consistency
 7. Limited capacity and seriality
 8. Sensory binding
 9. Self-attribution
 10. Accurate reportability
 11. Subjectivity
 12. Focus-fringe structure
 13. Consciousness facilitates learning
 14. Stability of conscious contents
 15. Object and event-centered
 16. Consciousness is useful for voluntary decision making
 17. Involvement of the thalamocortical core
-

Source: *Modified from Seth & Baars, 2008.*

During waking consciousness, the thalamocortical system reveals a constant flow of signal traffic, with thousands of messages going back and forth. Figure 8.3 shows a large-scale simulation of the known neurons and synaptic signal flow in the thalamocortical system (Izhikevich et al., 2004, 2008).

Waking consciousness resembles the back-and-forth flow of traffic in a busy city. At night, street traffic might dwindle to a few cars, but during the rush hour, vehicles are constantly going from any location to any other. It is that ability to go anywhere, guided by local goals, that makes cars useful. Waking tasks serve a huge variety of functions with great flexibility.

Humans have access to a remarkable range of conscious events—the sight of a single star on a dark night, the difference between the sounds “ba” and “pa,” and the goal of studying for an exam. All sensory systems do a great deal of unconscious processing, leading to conscious, reportable sights, sounds, and feelings.

Recalling an autobiographical memory also results in conscious experiences, like your memory of seeing this book for the first time. Inner speech and imagery have conscious aspects. Asking someone to rehearse a list of words usually results in conscious inner speech. People vary in the vividness of their visual images, but dreams are generally reported to have vivid imagery (Stickgold et al., 2001). Finally, action planning can have conscious components, especially when we have to make choices about our actions (Lau et al., 2004a, b). Normally, we may not have to think much about the action of walking, but if we injure a leg, even standing up and walking can become a consciously planned process (Sacks, 1984).

2.3 What we expect from conscious people

Table 8.1 presents 17 properties of consciousness that are generally recognized in scientific and medical literature. (Of course, the humanities, arts, philosophy, and religion have a long history of exploring consciousness, too.) People with head injuries are often given a mental status examination, which tests for abilities we expect normal, conscious people to have (McDougall, 1990). The test includes the following:

1. Orientation to time, place, and person: “What day of the week, date, and season is it?” “Where are you now?” “Who are you?” “Who am I?” (asked by the examiner)
2. Simple working memory: “Remember these three objects. . . .”
3. Attention and calculation: “Count down by sevens starting from 100.” (100, 93, 86, 79, 72 . . .)
4. Intermediate recall: “What were the three objects I asked you to remember a few minutes ago?”
5. Language: Asking the patient to identify a wristwatch and a pencil, to repeat a sentence, to follow three simple commands, to read and understand a simple sentence, and to write their own sentence.
6. A basic visuomotor skill: Asking the patient to copy a drawing of a line pentagon.

The mental status exam gives a broad overview of normal mind and brain functions. Some disorders involve disorientation, others affect short-term memory, and still others impair visual and motor coordination.

We also expect healthy, conscious adults to do *realistic thinking*. While dreams are unrealistic, waking consciousness has been believed to be necessary for logical, mature, and reality-oriented thought. Nevertheless, we routinely experience waking fantasies, unfocused states, daydreams, emotional thinking, and mind wandering.

2.4 Waking has conscious and unconscious threads

It is important to keep in mind that waking cognition is woven of *both* conscious and unconscious threads, constantly weaving back and forth. For example, the process of reading *these words* is only partly conscious. You are a highly practiced reader, and you have learned over

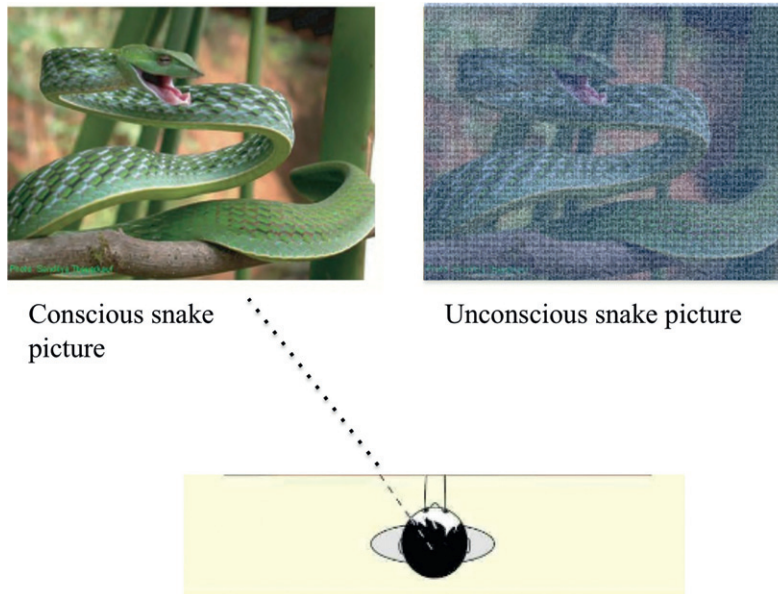


FIGURE 8.9 Comparing conscious versus unconscious events during the waking state. The subject can report the snake on the left side but not on the right side, even though the experimental stimulus is identical. This can be done using binocular rivalry, for example. In this experiment the emotional brain (the amygdala) can recognize the unconscious snake. Humans evolved in environments where deadly snakes were not unusual. Source: Ohman et al., 2007.

many hours of practice to automatically convert *these tiny marks on paper* into your own inner speech and then into unconscious processes like word recognition, grammar, and meaning.

We do not become conscious of every mental step in reading a sentence. In fact, there is a great deal of scientific evidence today that all cognitive tasks have many conscious and unconscious components. Figure 8.9 shows an example of unconscious detection of the picture of a snake. Human beings are attuned to detecting some things unconsciously, it seems, including snakes and even facial expressions, which are processed through the visual system, and trigger the fear-sensitive amygdala, a major subcortical center for processing emotions.

One can imagine how that ability may have evolved, since humans (and our ancestors) lived for millions of years in environments where snakes were an everyday, deadly threat. Human beings learn a vast amount of information from other people, such as the danger of crossing busy streets without looking. We are not innately attuned to cars rushing through a street, although we may be afraid of “looming” objects like a fast-approaching elephant.

Until recently, however, the evidence was still hotly debated on whether humans respond to genuinely unconscious stimuli. Studies like this one seem to prove the point convincingly (see Figure 8.9) (Ohman et al., 2007).

Even conscious sensory percepts have stages of unconscious processing (Figure 8.10). We have both psychological and brain evidence to that effect. Social psychologists like Banaji and Greenwald (1995) have found evidence that social perception and inference seem to have unconscious properties as well.

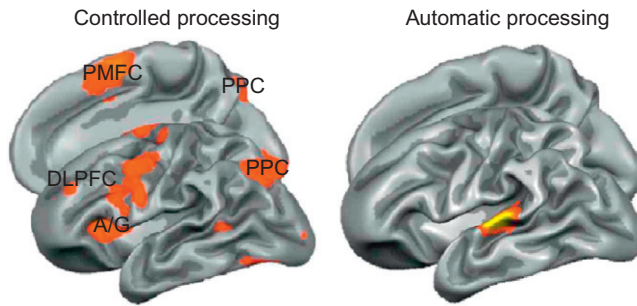


FIGURE 8.10 Voluntary and automatic skills. The brain images show cortical activity during two identical behavioral tasks. The difference is that the left-side task is novel and therefore requires more conscious and voluntary control (labeled “controlled processing”). The red-orange regions indicate fMRI peak activity mainly in the prefrontal and parietal lobes. The brain images on the right only show activity in the auditory cortex, probably because the specific auditory stimulus is never entirely predictable. Just like riding a bicycle, the most predictable parts of a practiced task tend to fade from consciousness. Instead of controlling every movement, we control higher levels, like which direction to steer. PMFC = premotor frontal cortex; PPC = posterior parietal cortex; DLPFC = dorso-lateral prefrontal cortex; A/G = anterior gyrus. Source: Scheider, 2009.

Almost all cognitive tasks we know take place during the waking state and have both conscious (reportable) and unconscious (nonreportable) components. Most cognitive tasks we know are therefore *consciously mediated*. Working memory, for example, has both conscious and unconscious components. If you rehearse seven numbers, you will notice that some are conscious at any moment, but others are not. The instructions to rehearse and remember are obviously conscious and so is the set of items as you see or hear them. But we are not aware of the nonrehearsed items at any moment, of the important role of the basal ganglia in controlling inner speech, or of the automatic (habitual) components of any task. There are no completely conscious cognitive tasks, as far as we know, and there may be no completely unconscious ones (Baars & Franklin, 2003). (Franklin has suggested the term “consciously mediated” for cognitive tasks that have a consciousness but are otherwise unconscious.)

The basal ganglia and cerebellum are very large brain structures that are believed to function without supporting moment-to-moment conscious contents, even in the waking state. The cerebellum can actually be lesioned on both sides and people will continue to behave much as before but without the ability to control fine motor movements. In humans those structures have many other cognitive roles but without direct conscious contents.

What can we do completely unconsciously? We still do not know the answer, because it is difficult to do careful studies on sleepwalking, sleep movement disorders, epileptic “automatic behaviors,” and other “zombie states” (Crick & Koch, 2003). There are many reports about automatic behaviors from individuals with sleep disorders and epilepsy. To verify those reports we need brain recordings that are difficult to obtain in freely moving people. It is also possible that epileptic behavioral automatisms, for example, reflect momentary conscious “flashes” that are known to exist (Kranczioch et al., 2006). It is therefore hard to test whether there are complex but entirely unconscious behaviors, in part because we simply do not know the distinctive brain correlates of consciousness as yet (but see Gaillard et al.,

2009; Revonsuo, 2006). We do not know yet what difference enables consciousness of the ventral but not the dorsal stream of the visual cortex. There are, however, ongoing efforts to answer those questions (Laureys & Tononi, 2008).

Most cognitive tasks we know are therefore consciously mediated. *Problem incubation* is a famous example of unconscious mental processing.

2.4.1 Task-related signaling between linked neurons

Because new findings about brain rhythms for cognitive functions are constantly appearing, it helps to use just three ranges: slow, midrange, and fast. Slow oscillations include the delta waves of deep sleep (less than 4 Hz). Delta waves are important for consolidating temporary memories into long-term memories. (In addition, a slower rhythm has been discovered that continues throughout the 24-hour cycle (Steriade, 1997).) There is no certainty yet about their role in waking tasks.

Delta waves occur during sleep and drowsy states, and similar slow waves occur during light anesthesia and in epileptic loss of consciousness. These are unconscious states. Faster waves occur during waking and dreaming.

MID-RANGE AND FAST WAVES

Cognitive tasks during waking are known to involve both midrange and faster waves. Until the evidence settles down, therefore, it is useful to talk about two frequency ranges for waking cognition.

ALPHA AND THETA RHYTHMS

Midrange oscillations include theta and alpha waves. Alpha rhythms of 8 to 12 Hz were first observed over the occipital cortex when human subjects were relaxed or closed their eyes. However, alpha and theta (4–7 Hz) are now known to be involved in many different waking tasks in many parts of the brain. In many cases these near-10 Hz waves seem to coordinate faster oscillations. In a very broad sense, near-10 Hz waves may function as a widespread “system clock” for many parts of the brain. For example, theta waves are known to facilitate encoding of temporary episodic memories into long-term episodic memory. In the motor cortex alpha-like rhythms have been reported to be involved in the inhibition of planned actions. In the frontal lobe, alpha-like waves are involved in momentary memory storage, and some researchers find that both synchrony and desynchrony of alpha waves may play a role in cognitive processes. Even the boundary between theta and alpha is not necessarily clear, and some researchers believe that these waves are not necessarily stable in their conventional range.

Scientific periods of rapid discovery often seem confusing until they settle into some stable pattern of evidence. Because empirical science is unpredictable, we do not know at this time whether the brain wave spectrum will be divided up neatly into frequency ranges or whether different brain locations will turn out to have quite different oscillations.

There is reasonable agreement, however, that alpha/theta oscillations near 10 Hz interact with faster oscillations. One proposal is that brain waves resemble the radio spectrum, with “carrier frequencies” being modulated (by amplitude, as in AM radio), or by frequency (FM). In the case of radio waves, broadcasting stations generate electromagnetic radiation at specific tuning frequencies (as you can see on your AM or FM dial). Radio receivers can be

tuned to the major frequencies. Since speech and music involve faster oscillations, these are “carried” by the standard tuning frequencies.

In the case of the brain, it is believed that theta waves sometimes work as carrier waves and that individual neurons can tune their own firing patterns relative to some widespread theta wave (Canolty et al., 2006). Since these are open issues on the scientific frontiers, we simply do not know precisely how they will settle over the longer term.

There is no agreement currently on the range of faster oscillations, often called beta and gamma. Functional rhythms have been reported up to 200 Hz and even (briefly) 600 Hz. Because new findings are constantly appearing, it makes more sense to describe three frequency ranges (see [Figure 8.1](#)). Midrange oscillations include classical alpha and theta, near 10 Hz. The pace of new findings is now so rapid that we can expect to see much greater clarification on these issues.

A range of frequencies have now been observed for sensory processing, attentional enhancement of sensory input, and both working and long-term memory. Synchrony is both natural and useful for signaling in an oscillatory system like the brain. Sometimes perfect synchrony is not attainable, so there is a brief time lag between the peak of the wave in one place (like the hippocampus) and another place (like the frontal lobe). In those cases, the better term is *phase locking* or *phase coherence*, a little bit like a syncopated “off-beat” rhythm in music. It is synchrony with a time lag.

Individual neurons have a temporal integration time of about 10 ms, the period when dendritic inputs can add up to increase the probability of a single axonal output spike (see [Chapter 3](#)). A group of interconnected neurons can strengthen one another’s firing rates between 30 and 100 Hz by supplying synaptic inputs within the 10 ms window. If two excitatory neurons are signaling each other at a rate of 50 Hz, for example, it is possible to sustain an excitatory feedback loop, because converging signals can arrive within the critical 10 ms period. However, neuronal firing rates below 30 Hz may not be integrated by target neurons because different spikes may arrive too late to have additive effects. It is therefore believed that a group of neurons firing in the beta-gamma range will exert a stronger drive to downstream neurons than lower frequencies. Obviously, real brain networks are more complex and have inhibitory as well as excitatory elements. Nevertheless, these basic points apply to neurons in general and have gained a good deal of direct empirical support.

Radio transmission has some similarities to oscillatory synchrony in the brain. The existence of AM and FM radio suggests at least two ways in which brain rhythms may process information in the brain. But there are many more coding schemes. Brain rhythms could serve as clocks, and they can use single pulses or a series of pulses like Morse code. Different neurons may use signals in different ways, perhaps in combination with different molecules and synapses.

Television is an example of a spatiotemporal code, in which the broadcast signal scans across every line of the screen from top to bottom. Computer screens use similar spatiotemporal coding. Brain rhythms are also likely to coordinate visuotopic maps, somatotopic maps, and motor maps. As we have mentioned, the brain is rich in topographical maps, which represent sensory input arrays or neuromuscular maps at various levels of abstraction (see [Chapter 5](#)).

Evolution has exploited the rhythmic properties of neurons over hundreds of millions of years. For that reason, we should not expect to find only a single neural code. What we do know is that brain rhythms are very widespread and that they are associated with known functions.



Finally, waves can also interfere with one another. When you place a radio receiver next to a computer, you will hear a burst of noise whenever you press the keyboard. That is because each key press triggers an electromagnetic signal that radiates into the surrounding space. Wave interference is a fundamental phenomenon in the physics of radiation. Interference may have important uses in the brain, but it might also degrade neural information processing. We are only beginning to understand the role of brain rhythms, but it is likely that wave interference will turn out to have effects as well.

3.0 ATTENTION

Common sense makes a distinction between attention and consciousness. The word *attention* seems to imply an ability to bring something to mind. If you can't remember a word in this book, for example, you might try to "pay more attention." What trying to pay more attention comes down to is allowing the forgotten word to be in consciousness for a longer time. So we rehearse the forgotten word (consciously), or we make a note about it (making it conscious again), or we write a definition about it (same thing). The traditional "law of effect" about learning states that the more we make something conscious, the more we will learn it. When we call someone's attention to a speeding car, we expect him or her to become conscious of it.

In everyday language, "consciousness" refers to an experience—of reading this sentence, for example, or conscious sensory perception, conscious thoughts, feelings, and images. Those are the experiences we can talk about to one another. Selective attention implies a selection among possible conscious events. When we make an attentional selection, we expect to become conscious of what we've chosen to experience.

With careful studies we can separate the phenomena of attention and consciousness. To focus on conscious events "as such," we typically study them experimentally in contrast with closely matched unconscious events, as we have seen in previous chapters (see [Chapters 1, 3, 6, and 7](#)). By contrast, experiments on attention typically ask subjects to select one of two alternative stimuli. "Attention" is therefore concerned with the process of selection and consciousness, with reportable experiences themselves. Some key questions for cognitive neuroscience are: What is distinctive about conscious events in the brain? What does it really mean for someone to be conscious? How does the brain basis of attentional selection relate to our private, conscious experiences of the world?

3.1 Attention selects conscious events

Attention has two aspects: the source of attentional control, which decides what to pay attention to, and the target of attention, which is selected for additional processing. Consider the case of a college student sitting in a lecture room, with many sensory inputs at the same time and many simultaneous tasks to perform. The student must stay alert, orient to the visual and auditory input, keep track of the lecture, take notes, and more. In fact, students are always multitasking, and as we know, that is inherently difficult. That is why it is important to review lectures. Live lectures can easily overwhelm our attentional capacities.

3.2 The Posner flanker task

Michael Posner and colleagues devised a simple method called the “flanker task.” They ask subjects to pay attention to a stimulus at a known location on the right or left side of the fixation point (marked with a dot or a plus sign) (Figure 8.11). Because humans have a very limited foveal “keyhole” through which they fixate a small part of the visual field at any single moment, it is possible to control the exact information that is available to a subject. (We see only about 3–6 degrees of visual arc when the eyes are fixed on a point. Try it!

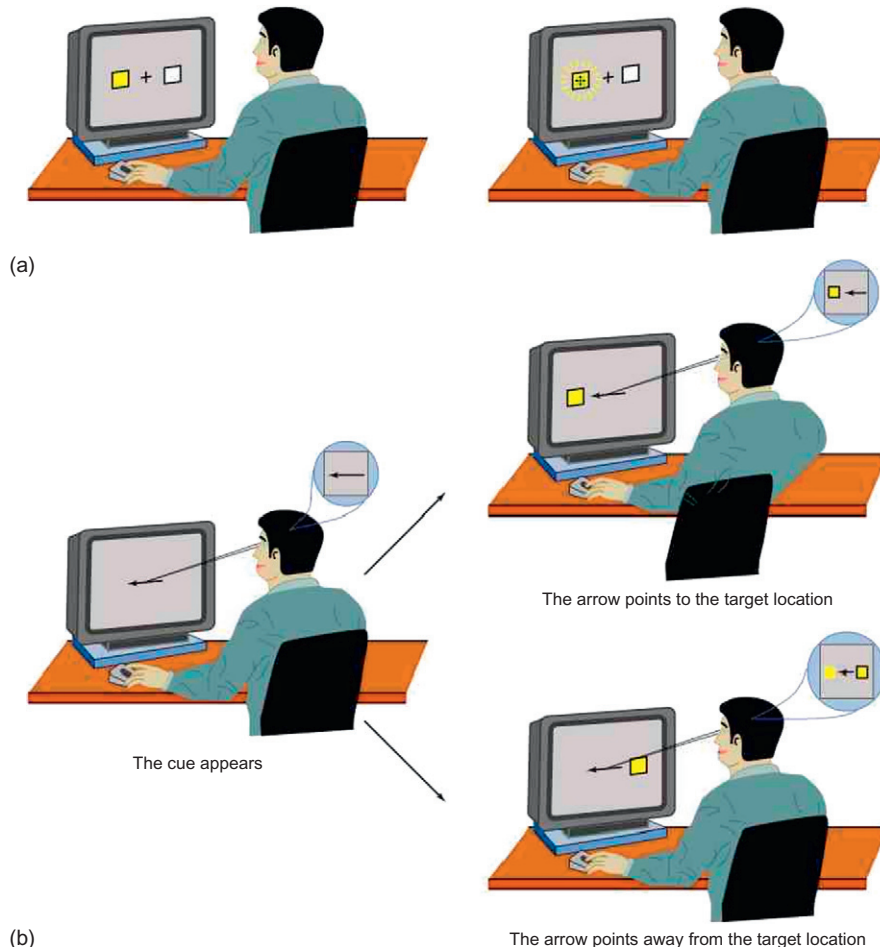


FIGURE 8.11 The flanker task for studying attention. The Posner flanker task has long been used to assess visual attention and its brain bases. The subject looks only at a fixation point in the center of the screen (a) Directional cues such as an arrow (b) draw attention to the left or right flank (side) of the fixation point, but no eye movements are allowed. It is the subject’s attention that is cued to one or the other side of the screen, not the eyes. Source: *Reynolds et al., 2003*.

The flanker task is simple, effective, and adaptable. For example, the target stimuli can be emotional faces, allowing us to explore how the brain pays attention to emotional events (Fan et al., 2002; Posner & Petersen, 1990).

Subjects keep their gaze on the fixation point. When flanking stimuli appear on the right or left side, they can be detected even when the eyes are kept fixed on the crosshairs. In [Figure 8.11](#), the target is flashed in the expected location for a fraction of a second. Subjects respond as quickly as possible. When their cued expectations are correct, their reaction times and accuracy are optimal.

The flanker task allows for testing of both voluntary and nonvoluntary attention, by giving subjects either correct or incorrect information about the flank on which the stimulus will appear. The task is simple enough to administer in an fMRI scanner in a half hour or so, and the resulting brain scans provide separate information about expectation-driven trials and unexpected trials. By subtracting the “unexpected attention” brain activity from the “expected attention” scans, Posner and colleagues were able to obtain a relatively pure measure of the brain regions involved in voluntary visual attention.

3.3 A model of attention

Itti and Koch (2001) developed a model of attention that combines a number of important features. It shows a simplified layered concept of the visual system, with multiple topographic visual maps. The visual maps show line orientation, stimulus intensity (contrast), color, and salience. *Salience* is defined in terms of feature contrast in any visual map. In light-sensitive regions, it is the contrast between light and dark patches on the map. In motion-sensitive areas, like area MT, it may be a stable object against the background of a waterfall. A combined salience map may combine all the contrasting features into a single saliency map, one that reflects the unusual, unexpected, or noteworthy features of a visual scene at any level of analysis. A “winner-take-all” computation selects the most salient location on a combined map and inhibits competing locations. Obviously, salience can also be misleading; for example, when you are watching a visually exciting music video that contains a variety of attention-driving features, you may want to think about something else. You may have to *override* what is most salient at any moment.

Visuotopic neurons respond to optical stimuli at different levels of analysis (see [Chapter 6](#)). [Figure 8.12](#) gives us a convenient overview. Each layer of the pictured model by Itti and Koch responds to a particular feature of the stimulus: color, line orientation, contrast, and object identity. This is a simplification of the visual brain, which is far more complex and flexible and that must deal with complications such as the constant motion of the eyes and the head, the very narrow limits on foveal vision, and much more. But [Figure 8.12](#) helps to clarify our question.

Each visuotopic map is a two-dimensional mosaic of neurons with rather narrow receptive fields (see [Chapter 6](#)). We can therefore ask a more focused question: Does attention to some event or location enhance signal processing in the correct receptive field? If the watcher in [Figure 8.12](#) is hot and thirsty while wandering in the Sahara Desert, will his or her attentional system enhance visual processing for ice-cold mugs of beer located on the left side of his visual field? This question is much more specific and testable.

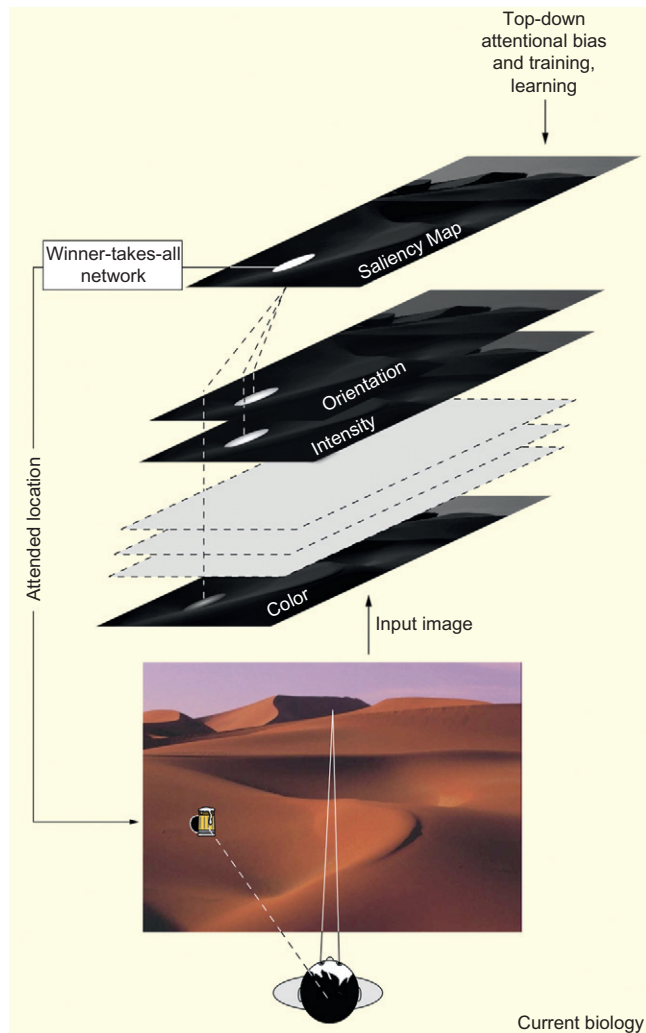


FIGURE 8.12 How attention might activate sensory maps. Multiple visuotopic maps support our conscious experiences of beer mugs and deserts. Notice that the person at the bottom seems to be looking for a cold drink on a hot day in the Sahara. How do our brains select the cold beer? What do we become conscious of? Source: Thier *et al.*, 2002; figure adapted from Itti & Koch, 2001.

The concept of a saliency map reflects significance, motivational relevance, and vividness of the input. Many topographical maps in the visual brain are sensitive to motivation and relevance. The man at the bottom of the figure is imagined standing in a hot desert with a cold mug of beer on the far left side of his visual field—just outside of his direct visual field. Selective attention allows significant stimuli like the cold beer to emerge into consciousness. These can be expressed as “top-down attentional biases” that alter the saliency map on top of the stack. Prior learning also is input into the saliency map. All the topographical maps resonate together in synchrony and jointly make decisions in cases where the corresponding points on the majority of maps lead to the same overall result. The output may be an eye movement, allowing the viewer to see the cold beer mug, or it may be a covert shift in attention to the left, again allowing

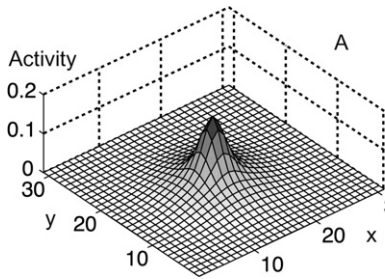


FIGURE 8.13 A winner-take-all (WTA) network, in which the most activated point in the horizontal plane inhibits all the surrounding points. The vertical axis is labeled *activity* and may represent the summed activity of multiple visuotopic maps. WTA networks are very common in decision-making neural nets. In the brain, both selective attention and conscious perception may make their final “decisions” using a WTA mechanism. In the case of ambiguous stimuli, the brain makes one of two competing interpretations conscious. Source: *Standage et al., 2005*.

the beer stein to come to visual consciousness. Again, it is possible that the man may want to override the perception of the cold beer and focus attention on crossing the desert instead. There are potentially competing decisions in this multilayered network.

An important aspect is the “winner-take-all” (WTA) network (Figure 8.13). WTA networks essentially allow the most active point on the joint topographical maps to “win,” input from saliency, which represents such things as motivation, hunger, and thirst; learning about relevance; and so on. WTA also suggests an explanation for conscious experiences of ambiguous figures. Conscious experiences are marked by internal consistency, even when sensory inputs are not. Most of the words in the English lexicon are highly ambiguous, for example, but in context (as in this sentence), ambiguous words are consciously experienced in terms of just one interpretation. Thus, a WTA network may be involved in an attentional system, as shown in Figure 8.12, but they are also a very powerful feature of conscious perception. Indeed, we can consider conscious perception to be the outcome of many attentional acts. In reality, there may be no difference in the brain between those two mechanisms.

The term *attention* is used most intuitively when there is a clear voluntary or executive aspect. We ask people to pay attention to things, which implies they can choose to do so or not, depending on some decision-making processes. Voluntary attention is the kind that is studied most often, and as you might guess from the other chapters, it is likely to use prefrontal cortex in humans (see Chapter 12).

Corbetta and colleagues (2002) recently wrote that voluntary attention “is involved in preparing and applying goal-directed (top-down) selection for stimuli and responses.” Automatic attention, on the other hand, “is not involved in top-down selection. Instead, this system is specialized for the detection of behaviorally relevant stimuli, particularly when they are salient or unexpected.” When we hear a sudden loud noise, our attention is “captured,” even without executive guidance. As you might expect, visual attention can be captured by human faces, emotional expressions, and bodies, when compared with neutral stimuli. Intense or sudden stimuli, or unexpected events generate larger brain responses than control stimuli. Thus we can talk about “bottom-up” capture of selective attention, driven by stimuli.

In the real world, voluntary and automatic types of attention are generally mixed. We can train ourselves to pay attention to the sound of the telephone ringing. When it rings and we suddenly pay attention to it, is that voluntary or automatic? Well, it began being voluntary and became more automatic. The dimension of voluntary versus automatic attention is therefore a continuum. Perhaps the strongest case of voluntary attention is the one where we must exert intense mental effort over a period of time. A clear example of the opposite pole of the

continuum might be a case of a loud sound or a biologically important event like a crying baby, which is hard *not* to pay attention to.

Therefore, attention is defined here as the ability to select information for cognitive purposes. Selection may be shaped by emotion, motivation, and salience, and it is at least partly under executive control. Thus selective attention works closely with all the other components of our framework diagram (see the chapter opening figure). Without flexible, voluntary access control, human beings could not deal with unexpected emergencies or opportunities. We would be unable to resist automatic tendencies when they became outdated or change attentional habits to take advantage of new opportunities.

As [Figure 8.14](#) shows, attention is a selective capacity, either under voluntary control or driven by a stimulus. The result of selective attention is to enhance the quality of the selected information or at least try to do so. What is the evidence for attentional enhancement?

[Figure 8.15](#) shows a current set of hypotheses about specific brain regions involved in voluntary attention to a visual location or stimulus. Notice that voluntary control of attention is attributed to the prefrontal cortex. Top-down activity descends to visual maps related to eye movements (prefrontal eye field, parietal eye field, and superior colliculus) and visuotopical feature maps (V1-IT). The pulvinar nucleus of the thalamus also contains a visuotopical map and is hypothesized to bring together saliency cues, basically representing contrasting features and their locations in all the sensory feature maps. Notice that this brain model lacks a WTA mechanism, as postulated by the abstract model shown in [Figure 8.13](#).

Top-down attention is driven by expectations, and in the delay interval (see [Figure 8.16a](#)) subjects know where to look, but the stimulus has not yet appeared. Yet visuotopical synchrony still occurs in motion-sensitive areas and the posterior intra-parietal sulcus (pIPS) on the right hemisphere. During this period of attentional expectancy there is significant coupling between MT and IPS. After the delay, the stimulus is presented to one side of the visual field, so its first effect will occur on the *opposite* side of the stimulus. If subjects know when to expect a visual stimulus, anticipatory synchrony occurs ([Figure 8.16](#)).

[Figure 8.17](#) shows that visual maps often synchronize, but that they synchronize differently in different tasks. Sometimes the frontal eye fields (FEF) are not in sync with other visual maps. You can imagine a rock band with players who are in sync some of the time, but not all the time. The vocalist might rest for a while and let other instruments take over, or different instruments might play in syncopation.

How is it that you can learn the material in this book? What we do in daily life is simply pay attention to new and interesting things—exploring them with our senses, rehearsing them mentally, and repeatedly directing our attention to them—and, magically, learning seems to occur. The next day, we suddenly realize that yesterday's new information seems more familiar. We must have learned it. Orienting tasks are important to enable learning. Mere exposure to information is often enough to enable recognition memory. In cognitive science jargon, most of our everyday learning is *incidental*.

What we generally do is just pay attention to new material, even if it seems hard to understand. The biggest challenge is paying attention to new and difficult information and be patient enough to allow our brains to wonder, ask questions, and, ultimately, comprehend any new material. Once we perceive and comprehend something new, learning seems to occur. Brain evidence indicates that spontaneous attention to some sensory content also activates the hippocampal complex (Stark & Okado, 2003). Though there is reliable evidence for

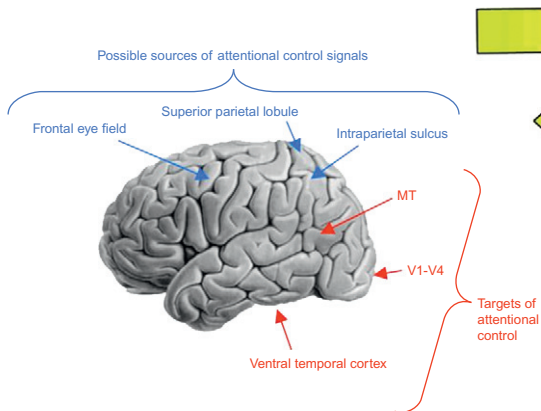


FIGURE 8.14 Voluntary attention. From frontoparietal to sensory cortex. Voluntary attention in perception is directed to sensory cortex by frontal and parietal regions. Parietal regions are believed to be involved in spatially directed attention. Visual regions (in red) are enhanced by attentional mechanisms, such as gamma synchrony among multiple visuotopic maps for the selected spatial location and visual features. Source: Yantis, 2008.

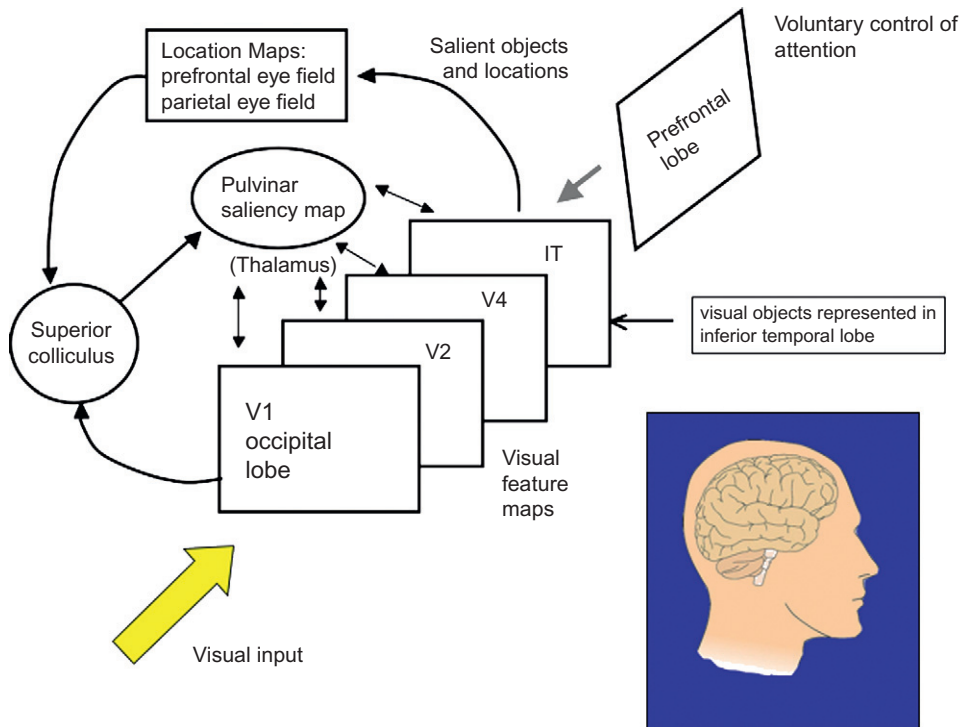


FIGURE 8.15 A brain model for visual attention. Shipp (2005) explores a number of brain models of visual attention. Notice that in addition to cortical maps, two subcortical maplike regions are shown. They are the pulvinar nucleus of the thalamus and the superior colliculus. Many of these same regions are involved in the control of overt eye movements, raising the possibility that in evolution visuospatial attention may have emerged on the prior basis of selective eye movements. Source: Adapted from Shipp, 2005.

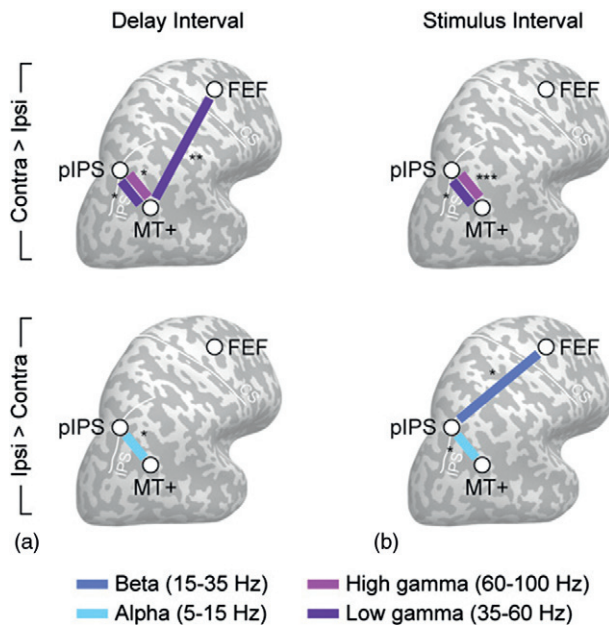


FIGURE 8.16 Attention works by synchronizing multiple visual maps. Here the MEG signal shows high synchrony in the right hemisphere. The cortex has been mathematically “puffed up” to make its hidden valleys (sulci) visible. Source: Siegel *et al.*, 2008.

subliminal perception and learning, we will limit this discussion to episodic and declarative memory of conscious events.

Cognitive neuroscientists believe that declarative and episodic learning occurs something like this (Seitz & Watanabe, 2005): We pay attention to new information so that it tends to become conscious. As soon as we experience the new information with enough clarity, our brains are able to store it. Repeated attention to new or difficult material often is needed before we get a sense of clarity. By using sensitive measures of episodic and declarative (conscious) memory, like recognition measures, we can show that humans learn very quickly after clear conscious experiences of new information. There is reliable evidence for subliminal learning, but here we will focus on learning of conscious events.

That does not mean we can recall all memories on cue. It does mean that we can recognize consciously experienced events far above chance.

For example, you may recognize a scene in a movie you may have seen ten years ago. It wasn't necessary to memorize the movie scene. All you had to do was to watch it once—consciously—and then see it again ten years later. Consciousness of an event seems to be enough to establish it in memory. Much the same is true of recognizing yearbook photos of high school classmates, news photos, headlines from years ago, and the like.

Unfortunately, academic exams rarely use recognition tests. Rather, exams test associative recall by asking questions like “What is the capital of France?” College exams would be easier if they gave us a part of the answer, like the partial recognition item “Par__ is the capital of France.”

Associative recall tests give much lower memories than recognition tests. That is why academic exams are difficult. It is not our stored memories that are at fault but our ability to retrieve them on demand. By analogy, you can file a book randomly in a giant library. The book (the memory) is somewhere in there, but you cannot retrieve it on demand unless

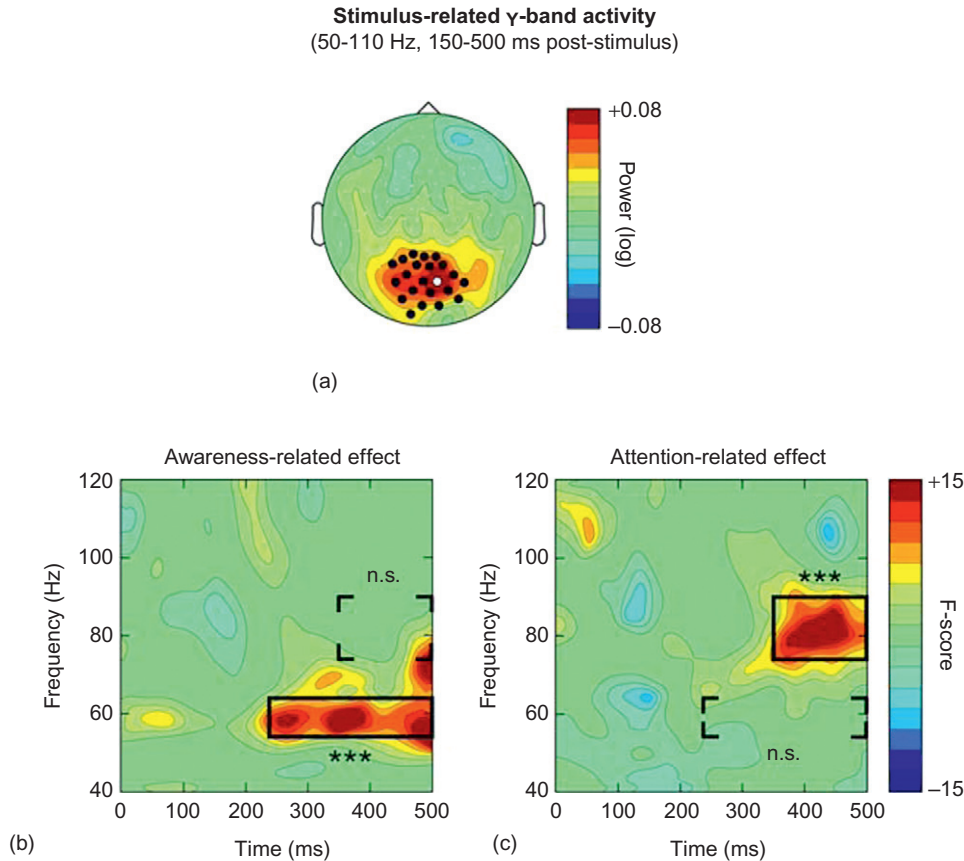


FIGURE 8.17 Separate brain correlates of attention and awareness. Wyart and Tallon-Baudry (2008) were able to dissociate the effect of visual awareness and selective attention. (a) MEG activity in the back of the brain (occipital) is shown in a simplified cartoon of the brain, as seen from above. The color bar shown on the right side indicates the intensity of the MEG signal. (b) Awareness has a different effect from selective attention. This figure shows MEG frequency on the vertical axis, with time on the horizontal axis. The zero point of time corresponds to the onset of the stimulus. We can see a burst of intense MEG activity around 60 Hz, starting 230 ms after the stimulus, and going on for several hundred milliseconds. In panel (c) we can see a separate attention effect at a higher frequency and starting a little later. Awareness and attention therefore seem like two different processes. Source: Wyart & Tallon-Baudry, 2008.

you have a very good retrieval system, like a search engine or a card catalog. Otherwise, the book might as well be lost forever.

Paying attention does not always make things conscious. For example, we can pay attention to an ambiguous figure without seeing interpretations (see [Chapter 1](#)). Learning a complicated subject like brain science is often like learning an ambiguous stimulus. At first, new material may seem vague, hard to understand, or confusing. Then we may spend some time thinking about it, paying attention to it, trying to draw it by hand, or answering questions about it. Over time, a clearer sense of meaning tends to come. At the point when we become clearly conscious of the information, learning tends to follow quickly. Most of our effort in studying new material is therefore devoted to the task of comprehension. Once we understand things clearly, memory tends to come along.

In sum, paying attention may be a means toward conscious clarity, which in turn enables learning. The hippocampal complex is believed to turn conscious experiences into memories. At first, hippocampal memory is believed to be unstable. Consolidation serves to make long-lasting changes to the neocortex. Theta oscillations play a role in local hippocampal functions and in long-range coordination between the hippocampus and neocortex.

3.4 Voluntary attention

Voluntary selective attention is controlled by the frontal lobes (executive functions) and parietal regions (for spatial localization, which is often needed for paying attention). The network of cortical and other areas has been called the *cognitive control network*. In the case of vision, many of these areas overlap with the control of eye movements.

If we want to pay attention to a spoken word in a stream of words, we may want to increase the sensitivity of our auditory and speech perception cortex to words that sound like “cognitive control network.” If we are reading, we want to do the same thing to visual word recognition areas. In general, therefore, we can think of the control of attention and the targets of attention.

One way to increase the signal strength in cortical area is to synchronize it. (See [Chapter 2](#) on neural synchrony.) The idea is similar to volume control on a loudspeaker. Because the brain can be viewed as a very large collection of topographical arrays that oscillate together with other topographical arrays, selective attention may simply “dance together” with attentional target arrays.

For example, the attentional network discovered by Posner and colleagues may dance to the same beat as face-selective visual maps of the temporal lobe ([Figure 8.18a-d](#)). [Figure 8.18b](#) shows that the attentional influences could work by adding to the overall synchrony strengthens the red face signal and decreases the blue face activity by breaking up its synchronous activity. Finally, in [Figure 8.18c](#), a synchronous population can respond to a stimulus and may keep running for some seconds or minutes after the stimulus has ended. Synchronous wave activity can therefore store a temporary memory, but it may fade fairly quickly and may also be vulnerable to interference from other stimuli.

These are only some of the coding possibilities of synchronous neurons and populations. Obviously, these hypotheses require evidence, as we will see.

3.5 Synchrony enables attention

Gamma synchrony may amplify neuronal population amplitude because synchronized neurons can add to one another’s activity. Synchrony tends to increase the size of the signal in much the same way a microphone that picks up sounds from a loudspeaker will tend to amplify the signal over and over again. In biological systems, such self-amplifying feedback can never be allowed to run out of control for the same reason that sound systems can’t allow infinite self-amplification. Audio systems have control circuits to prevent amplifier feedback from overloading the speakers, not to mention the ears of the listeners. Epileptic seizures may actually represent the wrong kind of self-amplification of slow rhythms, interfering with normal brain functions and even leading to a loss of consciousness.

The raw EEG shows only the surface waves of a deep and turbulent ocean. Underneath the visible EEG there are multiple oscillatory streams interacting over a wide range of

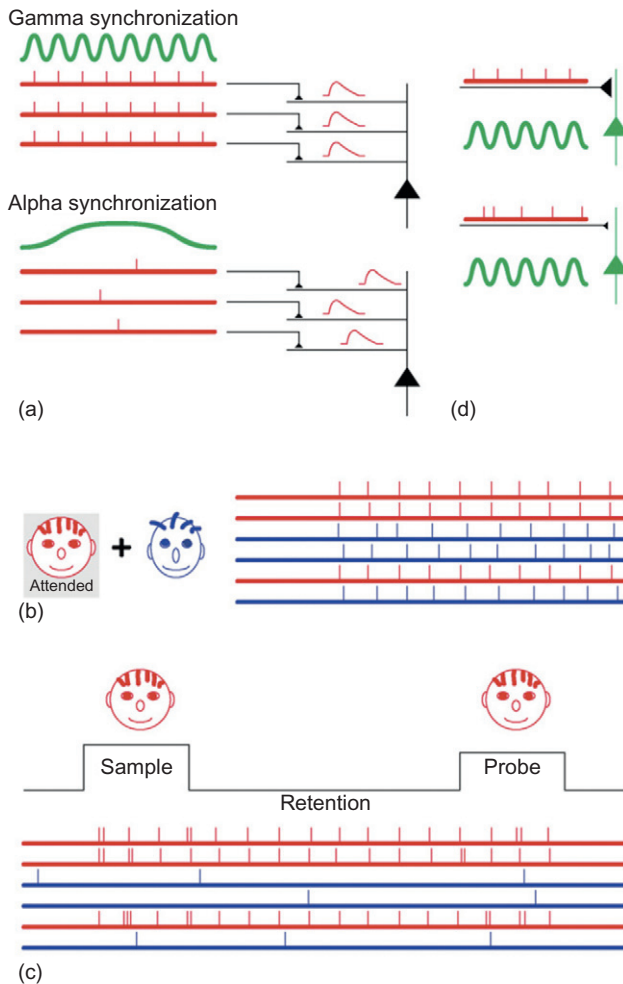


FIGURE 8.18 Synchrony in perception, attention, and memory. (a) Shows how several neurons firing at the same time can add up to a gamma wave in the electrical field. Gamma synchrony allows for finer temporal resolution than alpha. (b) Shows how attention might selectively drive target neurons at gamma rates. If you are looking at the red face on a sheet of white paper, neurons that are sensitive to the difference between red and white, those that fire to high visual contrast, and those that pick up faces will tend to fire in synchrony to enable the brain to encode the red face. If you then decide to pay attention to the red face, your brain can add to the activity of those sensory populations by firing additional cells in synchrony with the red face-sensitive populations. The blue face will not receive these additional pulses of activity. (c) Shows how synchronized neurons may retain a dynamic memory of a visual stimulus for seconds or minutes. The sample face triggers feature-sensitive neurons that fire in synchrony. When the sample face is removed, some of those neurons continue to fire for seconds or minutes. When the recognition probe is presented, the relevant neurons are already primed to respond to the recognized stimulus. There is direct evidence for such short-term memory mechanisms. (d) Shows how synchrony between single neuron firing and group oscillations can work to strengthen each other. Source: *Jensen et al., 2007*.

frequencies (0.01–1,000 Hz have been observed). Some of these under-the-surface waves are phase-locked. The metaphor of a turbulent ocean is a useful first approximation, but unlike the ocean there are many functional activities going on all the time. Knowledge about brain rhythms is building at remarkable speed.

4.0 EXECUTIVE CONTROL

The waking state supports an endless set of adaptive functions. One of the most important is executive control (see [Chapter 12](#)).

Intuitively most of us believe that conscious experiences involve an “experiencing I”—a personal viewpoint on the world that may be supported by parietal and prefrontal areas

of the cortex (Baars et al., 2003) (see [Chapter 12](#)). In daily life we use phrases like “I’m awake,” “I see the coffee cup,” “I lost consciousness,” “I couldn’t control myself,” and so on.

For many years the “observing I” was criticized as “the homunculus fallacy” (from the Latin word for “little man”). The problem, according to the critics, is that to make sense of the observing self, a little observer would have to sit in the brain, looking at the sensory inflow. But to make sense of the little observer, it would also need another little observer inside of it, and so on ad infinitum. Such an infinite regress does not explain anything. It just moves the burden of explanation to another level.

However, not all versions of an observing self lead to an infinite regress (Baars, 1988). For example, executive programs are routinely needed in robots, without leading to an infinite set of control routines. Similarly, it is possible to have an executive capability in the frontal and parietal lobes to interpret self-relevant information, such as “Is this new information good for me? If not, will it hurt? How much? Should I run away? Would I feel embarrassed if I did?” The emotions are generally believed to process self-relevant information, but even body movement requires the visual system to interpret a flow of visual vistas in these terms. Watching a visual flow while sitting still (in a car or in a theater) is not the same as actively walking or driving. Moving one’s eyes spontaneously is different from pushing the eyeball from the outside, as Helmholtz pointed out in a famous demonstration. The weight of scientific opinion may now be swinging back to the idea of an executive “I.”

There is a great deal of evidence for an executive network in the human brain (see [Chapter 12](#)). The brain areas in the cognitive control network (CCN) are shown in [Figure 8.19](#), with connections—fiber tracts—that form the neural basis for the CCN. For example, certain kinds of brain damage seem to damage executive functions without necessarily impairing conscious perception. The classic case of Phineas Gage involved a radical change in personality and impaired self-control. The sense of agency in voluntary control is also

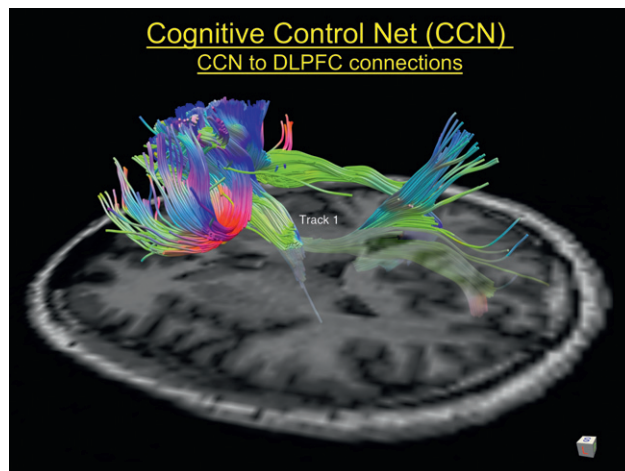


FIGURE 8.19 The Cognitive Control Network proposed by Cole and Schneider. The colored tracts are white matter fibers densely connected in the frontal lobes (on the left), and making parietal connections (on the right). The tractography images are in very high resolution. Source: W. Schneider, *personal communication*, 2009.

dependent on the frontal regions, and the right parietal region is a crucial area for “perspective of the self” in the neurological condition of parietal neglect (Baars, 2002; Baars et al., 2003).

4.1 Losing voluntary control

The outer muscles of the body and head are inhibited during sleep. Sleep-related muscle inhibition is easy to notice when your head starts to drop down when you feel drowsy. In your brain, a small circuit in the brainstem simply switches to its sleeping mode. It is now inhibiting body muscles. When you are awake, the same circuit maintains your upright posture and normal muscle tone. Muscle inhibition in sleep probably evolved to avoid sleepwalking or acting out one’s dreams.

5.0 DREAMING

Hobson and colleagues (2000) define dreams as:

Mental activity occurring in sleep characterized by vivid sensorimotor imagery that is experienced as waking reality, despite such distinctive cognitive features as impossibility or improbability of time, place, person, and actions; emotions, especially fear, elation, and anger predominate over sadness, shame, and guilt and sometimes reach sufficient strength to cause awakening; memory for even very vivid dreams is evanescent and tends to fade quickly upon awakening unless special steps are taken to retain it.

In a sense, dreaming is our most creative state. In normal waking we could never spin out the flow of visual scenes, dramatic characters, or strange plots we constantly make up in our dreams. It is almost as if we are creating a running movie but we can’t recall the storyline from one scene to the next. Spontaneous waking thoughts tend to be about our current concerns, and dream contents may refer to those concerns in a more visually symbolic way.

Both sensory input and muscular output are blocked during REM dreaming, so the brain is talking only to itself (Figure 8.20). The existence of muscular inhibition may give rise to some “paralysis dreams,” in which we feel paralyzed or want to move but feel we cannot. This can

TABLE 8.2 What Makes Dreams Different

1.	Hallucinations—especially visual and motoric, but occasionally in any and all sensory modalities
2.	Bizarreness—incongruity (imagery is strange, unusual, or impossible; discontinuity (imagery and plot can change, appear or disappear rapidly); uncertainty (persons, places, and events often bizarrely uncertain by waking standards)
3.	Delusion—we are consistently duped into believing that we are awake (unless we cultivate lucidity)
4.	Self-reflection absent or greatly reduced—relative to waking
5.	Lack of orientational stability—people, times, and places are fused, plastic, incongruous, and discontinuous
6.	Narrative story lines—explain and integrate all the dream elements in a confabulatory manner
7.	Emotions increased—intensified and predominated by fear-anxiety
8.	Instinctual programs—(especially fight/flight) often incorporated
9.	Volitional control—greatly attenuated
10.	Memory deficits—across dream-wake, wake-dream, and dream-dream transitions

Source: Hobson in Squire et al., 2008.

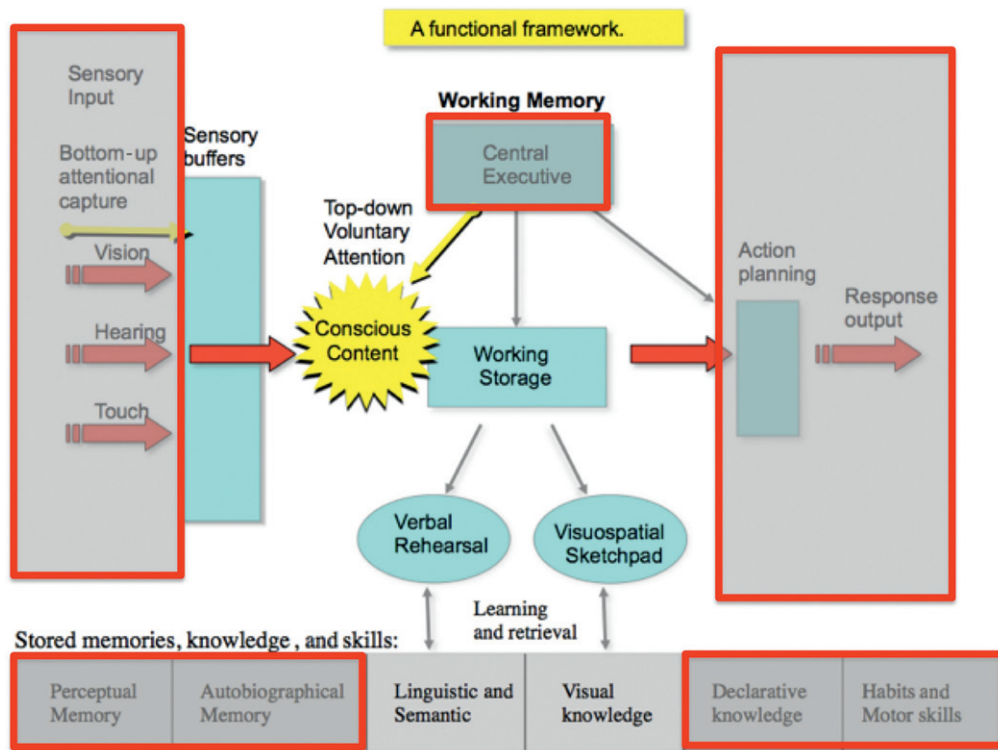


FIGURE 8.20 The grayed-out boxes show impaired functions, including sensory and motor flow, executive functions, and some kinds of memory. Dreams are conscious states, but voluntary control is lost. Visual imagery is unusually vivid. Source: *Baars, with permission.*

lead to unpleasant “locked-in” feelings during dreaming if we become aware of being unable to move. But muscular inhibition is an entirely normal part of dreaming. It keeps us from acting out our dreams.

Memory is also impaired during rapid eye movement (REM) dreaming. When dreamers are woken up from REM, they may report vivid visual memories, but they tend to fade in seconds unless we make a special effort to rehearse them. Even people with good dream recall are likely to remember only a tiny fraction of their nightly 90 to 120 minutes of REM (Figure 8.21).

5.1 Dreams are conscious

Dreams are reported as conscious experiences when people are woken up during REM. The EEG of REM dreaming is strikingly similar to wakefulness. It therefore seems that we actually have two daily conscious states: waking and REM dreaming. The activity of waking and dreaming reflects a similar operating style by the thalamocortical system. During dreams, the EEG looks very much like waking consciousness (see Figure 8.1). The function of dreams is still debated, but similar physiological states are found in many mammals.

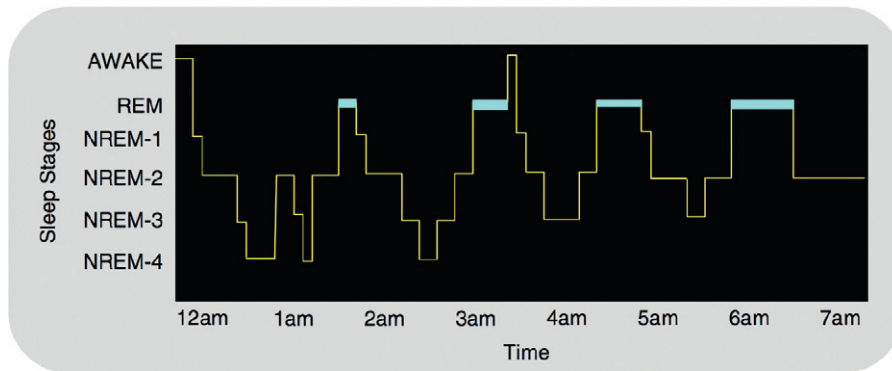


FIGURE 8.21 The architecture of sleep. The thalamocortical core changes dramatically in sleep. In deep sleep, the low, irregular oscillations of waking EEG change to high, slow, and regular activity, called *delta* waves. The four levels of arousability (Stages 1–4) show increasing delta waves, until Stage 4 of Non-REM (NREM-4) is almost all delta. Every 90 minutes or so, sleepers show rapid eye movements (REM) as the eyes swing back and forth. At the same time the EEG shows striking waking-like activity in the EEG: fast, irregular, and low in amplitude. People who are awoken from REM tend to report vivid, narrative dreams, whereas SWS sleepers may report waking-like inner speech. REM periods become longer in the second half of the night. Source: *Stickgold & Walker, 2007*.

Dreaming is therefore likely to have an evolutionary function. However, it is important to keep in mind that there are important differences during REM as well, such as sensory and motor blocking, a high level of emotional activity, and a low level of executive (frontal lobe) control.

5.2 Nonrational thinking

The surreal and nonrational nature of dreams may reflect this lower level of executive control. Dreaming is a “hypofrontal” state, like drowsiness, alcohol inebriation, delirium, and other states of lowered self-reflection and self-control (Dietrich, 2003). In addition, the limbic regions of the brain, which are involved with emotions, show higher fMRI activity than in the waking state (Figure 8.22).

5.3 Working memory in dreams

In dreams we can unexpectedly jump from one imagined scene to another, and dream characters can change their identities, as if the brain is constantly trying to reinterpret the flow of imagined experiences from moment to moment. Waking events tend to be much more coherent.

One possibility is that dreams overload our immediate memory with their creative flow of emotions, images, and imaginary encounters. If we tried to spin dreamlike fantasies during the waking state, we would certainly lose track of our narrative, just because it’s hard to remember all the details. Story writers work for hours and days to imagine what all of us experience from minute to minute during sleep. The jumpy transitions in dreams may reflect moments when we simply lose track of the plot.

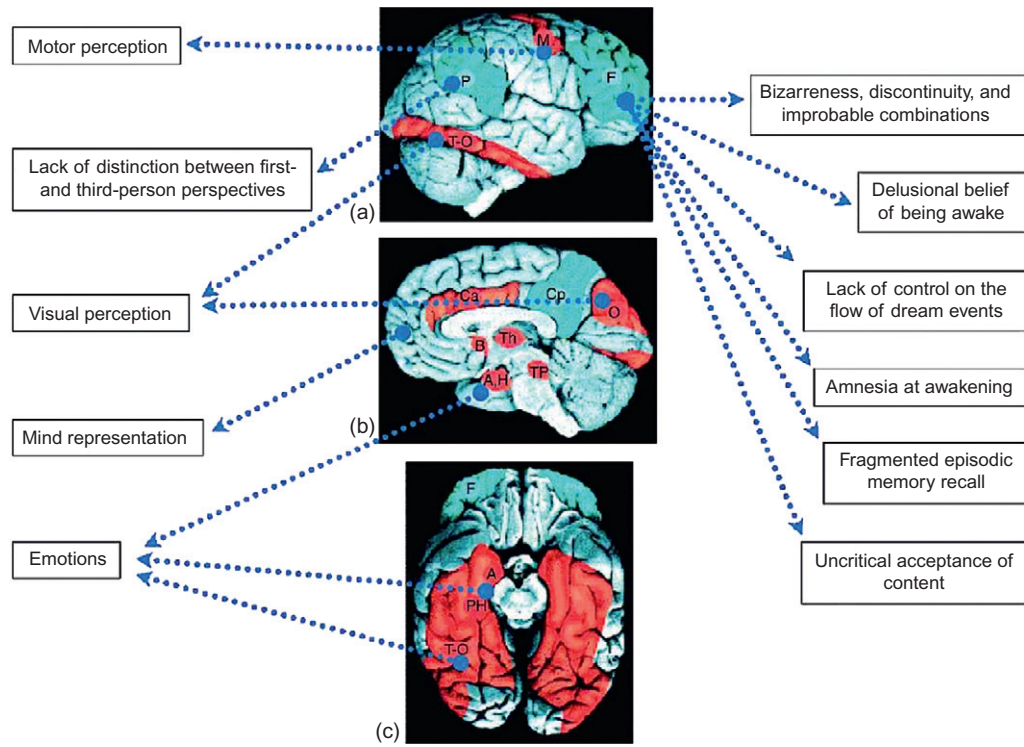


FIGURE 8.22 Functional brain imaging of REM dreams. Red areas represent increased blood oxygen-related activity—for example, in emotion areas. Blue areas correspond to below-baseline activity during dreaming, as in the frontal lobes. Higher activity in occipital regions may reflect vivid visual dream imagery. Low frontal lobe metabolism may also explain the delusional beliefs, bizarreness, and sudden discontinuities of dreams, such as rapid changes in scenes, dream characters, and narrative coherence. Low frontal lobe functioning is consistent with amnesia for dreams upon awakening and low levels of voluntary control. Source: *Dang-Vu et al., 2005*.

5.4 Brainstem oscillations trigger dreaming

REM dreaming is triggered by “PGO waves”—pons-geniculate-occipital activation—along with neuromodulation. Sharp bursts of neuronal spikes come from the pons (P), activate the lateral geniculate nucleus of the thalamus (G), and then trigger visual experiences by way of the occipital cortex (O). Hobson and McCarley (1977), who advanced the early PGO hypothesis, called this the “activation-synthesis hypothesis,” with the emphasis on the activation burst from the pons and its conscious interpretation or “synthesis” by the cortex (see [Figure 8.22](#)). Pace-Schott and Hobson (2002) write that REM sleep is also triggered by changes in major brain modulators, especially norepinephrine, acetylcholine, serotonin (5-HT), and glutamine.

However, the PGO theory does not explain the *content* of dreams. It only suggests that the cortex tries to make a coherent story out of meaningless brainstem signals. What determines dream contents remains a puzzle. Valli & Revonsuo (2006) proposed a “threat simulation” theory of dreams, an evolutionary hypothesis based on the fact that the REM state is widely observed in mammals and birds and therefore may have an important evolutionary function.

Valli & Revonsuo (2006) suggests that dreams allow us to mentally rehearse threatening situations. Traumatized individuals may re-experience events related to the trauma (in some cases even during the waking state). Consistent with their theory, Valli & Revonsuo (2006) found that traumatized children from a war zone had significantly more threatening dreams than controls. Other major life events, such as loss of a loved one, or even normal stressful events, might also be reflected in dream contents.

5.5 Lucid dreaming

Some people can learn to experience their dreams *knowing* they are dreaming, and even with some voluntary control over dream events. LaBerge and colleagues (1986) made a case for such “lucid dreaming” in the sleep laboratory by showing that some dreamers could learn to voluntarily move their eyes back and forth three times in a row, on cue, when given an auditory signal. Some lucid dreamers could also count to ten in the dream and then show the experimenters that they had done so by repeating the triple eye movement to signal the end of the ten-second period. Lucid dreamers in this experiment had to recall and carry out their task instructions learned during the waking period before going to sleep. Thus lucid dreaming required executive functions and semantic memory retrieval, as well as linguistic and auditory processing. Lucid dreamers may therefore be able to control some of the cognitive functions that usually are impaired in the REM state.

6.0 DEEP SLEEP: UPS AND DOWNS

Deep sleep is the least conscious state of the daily cycle. It is also called “slow wave sleep” (SWS) because of the predominance of slow EEG waves over the cortex during this time. (see [Figure 8.2](#)). In slow EEG, billions of neurons in the cortex and thalamus turn on and off in unison at the rate of the delta wave (about 2–4 Hz). The flow of signals is forced to screech to a halt every half second, then start again, stop again, and so on. The fast and flexible flow of signaling is therefore constantly disrupted. Unconsciousness is the state where we cannot perform our normal, waking activities because the engine of consciousness cannot maintain continuity.

Why do we sleep and dream for a third of the day? We only know a few of the answers. Deep sleep is the best time for consolidating what we learn during conscious periods into long-term memories. Sleep and dreaming probably have other functions. We know that hundreds of neuronal genes turn on and off whenever we fall asleep or we wake up. But there is no scientific agreement on the functions of our “offline” states.

Waking consciousness is the best time for learning, but learned material is “consolidated” during the next deep sleep period. If you study for an exam, it’s good to “sleep on it” and then refresh your memory in the morning. Much of yesterday’s learning will then be stabilized.

6.1 The need for sleep

Sleep-deprived rats die after only three weeks. We know therefore that sleep is needed for survival in rats and very likely in other mammals. Sleep duration is under precise biological regulation. We tend to make up for lost sleep by sleeping longer. Sleep-deprived individuals show

“microsleeps”—moments of “dropping off”—that can seriously interfere with actions like driving. In a second or two, your neck muscles can lose tone, and your head will tend to drop forward.

As a major biological adaptation, sleep presumably does things that help us to survive and reproduce as a species. Many of its functions are programmed genetically, causing DNA-controlled proteins to build new synapses to consolidate learning. And yet, sleeping animals are also more vulnerable to predators. Animals seek shelter before going to sleep, in trees, in earth hollows, or in dense bushes that are hard for predators to penetrate. Some animals rely on large colonies that sleep together so they can warn one another about predators. Nevertheless, sleep is still a period of special danger because animals cannot run, flee, fight, or engage in mate selection and reproduction.

Our nightly eight hours of unconsciousness must therefore have some compensatory advantages. We know that sleep seems to enable memory consolidation, converting new and unstable memories into lasting ones. The function of dreaming is still debated. Because the sleep-waking cycle is a very widely conservative feature among animals, it is likely to have multiple functions.

Surprisingly, a single night of sleep deprivation can also improve depression. Staying up for one night therefore has been suggested as a safe, inexpensive, and effective treatment. But chronic (long-lasting) sleep deprivation is stressful and degrades normal conscious functioning.

6.2 Memory replay and consolidation

SWS is more common in the first half of the night, whereas REM predominates in the second half. Researchers therefore have studied memory consolidation after “SWS-rich” and “REM-rich” periods of sleep. In general, SWS-rich periods appear to strengthen explicit memories, and REM-rich periods strengthen procedural tasks and perhaps implicit memories. Increased SWS has been observed after intensive episodic learning, and increased REM is seen after procedural training.

Episodic memories are thought to be transferred from the hippocampus to the neocortex for memories to become enduring. The hippocampus plays a major role in place learning and navigation, and it has been possible to pinpoint hippocampal “place cells” that fire when the animal passes a particular point in the maze. As the rat runs the learned maze, place cells fire in sequence. Afterward the same pattern of cell firing is observed during slow wave sleep, activating other parts of the brain, like the thalamus, neocortex, and basal ganglia (Figures 8.23 and 8.24).

In rats, we can actually record neurons when the animals are exploring locations in sequence and observe that the brain *replays* a learned spatial sequence during SWS. The theta rhythm appears to be a major rhythm for the hippocampal-neocortical dialogue that leads to memory consolidation (Buzsaki, 2006; Jensen & Colgin, 2007).

7.0 EXCEPTIONAL STATES OF MIND

To achieve altered states, humans have used a huge variety of methods: taking psychoactive plants, fasting, drinking alcohol, special exercises, visualization, disorientation, hypoxia, self-mutilation, sexual practices, dramatic rites, lucid dreaming, dancing, whirling, chanting and music, suggestion, trauma, sleep deprivation, and social isolation. Traditions like

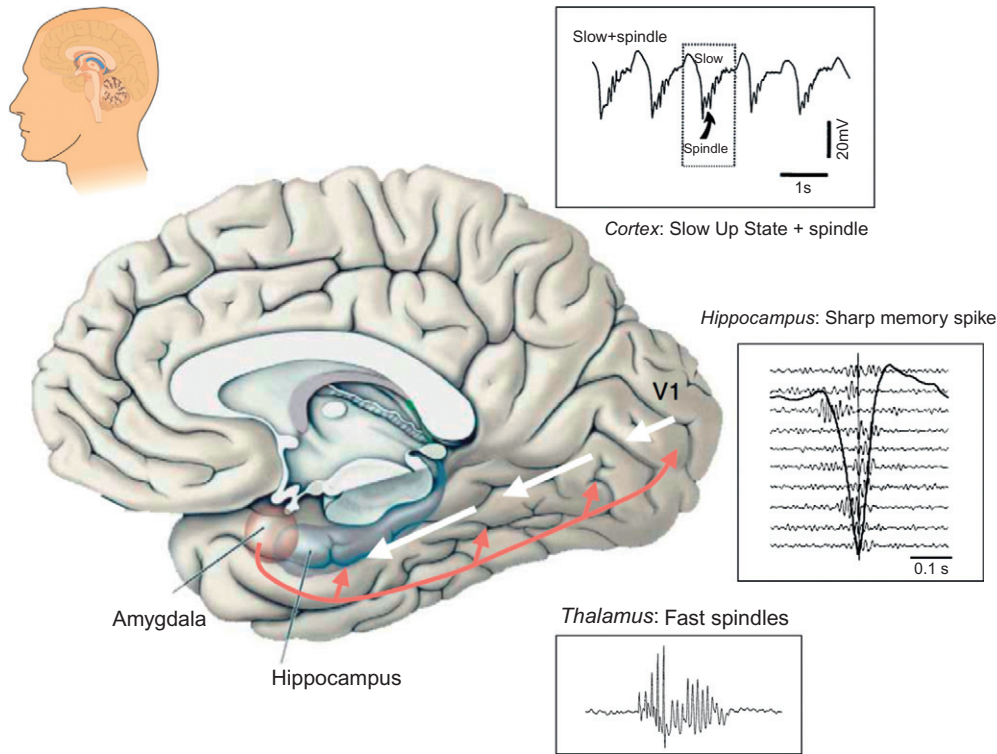


FIGURE 8.23 Slow wave sleep enables memory consolidation during “up states.” Three brain regions work together: early episodic learning during the waking state encodes unstable hippocampal and neocortical memory traces. During slow wave sleep, thalamic spindles ignite, which triggers hippocampal sharp spikes, which are believed to activate synchronized memory traces in the hippocampus. Thus thalamic spindle activity helps to trigger the next up state, as shown by cortical iEEG. These regions act in concert to reactivate recent memory traces. During the following down state of slow wave sleep, the activated neurons are believed to express proteins that lead to synaptic plasticity for more enduring memory coding. *Source: Adapted from Steriade, 2000.*

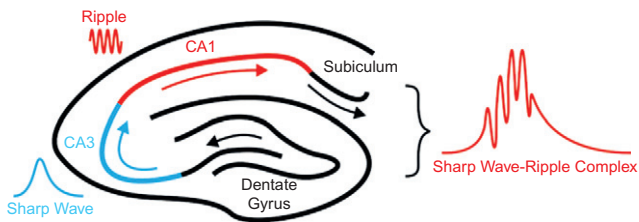


FIGURE 8.24 Hippocampal sharp and ripple waves. A cartoon of the hippocampus shows its basic arrays of neurons, which generate sharp waves and ripple complexes in activating retrieval and neocortical consolidation during slow wave sleep. *Source: Beenhakker & Huguenard, 2009.*

Buddhism and Vedanta Hinduism believe that humans should change their states of consciousness and self. That belief can be found in many times and places.

Simply asking people whether some practice makes them happier does not make for convincing evidence. Brain evidence may be more convincing. We cannot alter our EEG or fMRI scans to prove a favorite hypothesis. Decreased metabolism in the frontal lobes may be a

common theme for altered states. Dietrich (2003) argues that lowered frontal metabolism is a shared feature of hypnotizability, “runner’s high,” “flow,” and other unusual states of mind.

7.1 Epilepsy, drugs, and psychoses

Some mystical experiences are associated with epilepsy. Epileptic patients sometimes describe altered states as their EEG begins to show slow synchrony, even without visible seizures (see [Figure 8.8](#)). Since epileptic synchrony alters the workings of the thalamocortical core, there could be a link between altered subjective states and brain rhythms.

Psychedelic drugs have been compared to dreams, often showing vivid visual hallucinations, delusions, dreamlike actions, emotional encounters, time loss, and discontinuities. Similar experiences are described with some psychedelic drugs. The LSD molecule resembles serotonin, which is involved in REM dreaming. “Recreational drugs” by definition are taken with the goal of having unusual experiences. In the psychoses, delusions and hallucinations are often extremely upsetting, frightening, and unwanted. They occur at unexpected times, interfere with normal life, and can develop into painful persecutory voices and distressing beliefs. The degree to which these experiences are unwanted is one major difference between psychedelic drugs and psychotic experiences. Mental disorders are not a matter of choice, and people who suffer from them cannot stop at will.

7.2 Out-of-body experiences

Direct stimulation of the right posterior parietal cortex (PPC) can evoke dramatic changes in experienced body space ([Figure 8.25](#)), including out-of-body experiences (OBEs). Some of the most reliable results come from studies of OBEs, the experience of looking at one’s own body from the outside. Some epileptics experience alterations in body space, perhaps because of hypersynchronous activity affecting the parietal cortex. The parietal cortex plays a role in several unusual states.

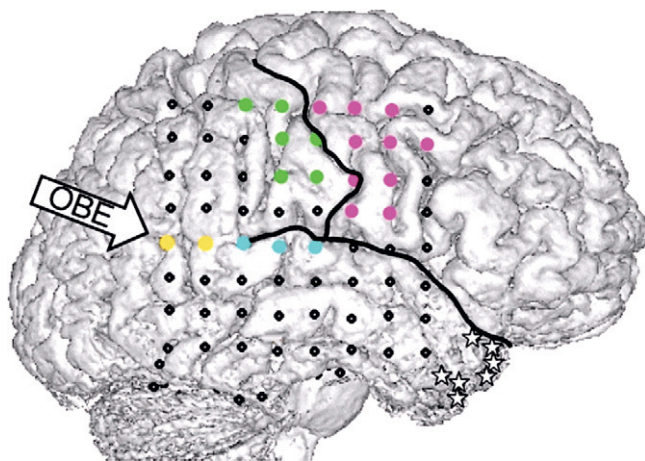


FIGURE 8.25 Electrical stimulation of the colored locations on the right parietal cortex and evoke out-of-body experiences. Source: Tong, 2003, after Blanke et al, 2002.

7.3 Neurofeedback

Neurofeedback training is defined as learning to control brain events by giving sensory (conscious) feedback, contingent on the event. Simply by holding a thermometer one can learn to increase warmth, for example, which seems to help people relax and lower blood pressure. Neurofeedback studies of animals have shown positive results over several decades. In a brain with billions of neurons, simple sensory feedback can allow training of voluntary control over otherwise involuntary neuronal firing.

EEG neurofeedback show significant results, but long-term studies are often lacking. Because neurofeedback may work in cases where other medical treatments have failed, long-term trials would seem to be vitally important.

7.4 Sensorimotor rhythm feedback

The sensorimotor response (SMR) is an alpha-like EEG pattern found over the motor cortex when people voluntarily suppress some planned action. SMR feedback training has been shown to be an effective treatment in cases of human epilepsy, ADHD, and impulse control disorders (Stermann, 2006). On average, 80 percent of patients trained to enhance SMR had significant improvements.

Drug treatments for epilepsy do not always work, and having another treatment is helpful for many patients. Scientifically, because epilepsy shows slow, synchronous, and high waves in the EEG, the ability to modify it by training reveals an interesting fact about the voluntary control of brain rhythms.

7.5 Rhythmic entrainment

If brain rhythms constitute a basic neural code, it would be interesting to know if we can drive rhythms externally. If we listen to a 10-Hz auditory stream, will alpha waves increase? Brain wave entrainment has been described with TMS (transcranial magnetic stimulation) and tACS (transcranial alternating current). However, although there are many popular claims about the effects of auditory entrainment, they have not been demonstrated to work by demanding medical and scientific standards so far.

7.6 Hypnosis and conversion

About one-fourth of the normal population is highly hypnotizable, as assessed by standard hypnotic procedures. Hypnotic suggestions can change brain events, as in reducing the averaged evoked potential (AEP) to a flashing light simply by “hallucinating” a cardboard box covering the stimulus (Spiegel, 2003). We do not know how hypnotic induction works. About 5 percent of the population are said to be “hypnotic prodigies,” who can hallucinate perceptual events, such as the buzzing of a fly; they can also enter into dissociated identity states (Hilgard, 1977). fMRI studies show that hypnotically suggested pain activates some of the same brain regions as real pain. Hypnotic procedures can alleviate chronic pain (Spiegel, 2003).

Hypnosis may involve a dissociation between voluntary control (dorsolateral prefrontal cortex, DL-PFC) and the ability to monitor errors (the anterior cingulate cortex, ACC). Egner and colleagues (2005) reported an fMRI-EEG study of hypnosis in the Stroop task showing that “hypnosis decouples cognitive control from conflict monitoring processes of the frontal lobe.”

Mild conversion symptoms are quite common in medicine. Medical students who are studying serious diseases may become worried when they seem to notice “real” symptoms in themselves. “Medical student syndrome” is common and generally fades over time. Conversion disorders might be a result of the general human tendency toward autosuggestion. The placebo effect is a positive version of autosuggestion.

7.7 Meditation and yoga

The term *meditation* covers many mental techniques. One is silent repetition of a word called a “mantra.” Asian and other traditions describe mantra meditation as a method for changing mind states, as taught in Vedanta, Buddhism, and Chinese medicine. It has also been widely practiced in Europe and the Middle East.

Meditation methods have been reported to increase coherence (synchrony), especially in theta, alpha, and beta-gamma EEG. Frontal-lobe coherence is also reported, as well as improved attentional functioning (Lazar et al., 2000; Lutz et al., 2004; Tang et al., 2007).

One of the surprises with mantra repetition is a significant drop in metabolic activity, reflected in “breath suspensions”—spontaneous stopping of the breath without compensatory breathing afterward. This is different from holding our breath voluntarily. In swimming, for example, we may take a deep breath before diving and then feel the need to take some extra breaths after coming up for air. The lack of compensatory breathing suggests that energy demand has indeed dropped more than an ordinary resting state, as has been demonstrated by measuring O_2/CO_2 exchange (Benson et al., 1975).

Herbert Benson and colleagues (1975) proposed that these results represent a “relaxation response,” like other physiological reflexes. Spontaneous breath suspensions are reported to be associated with reports of periods of “pure consciousness,” defined as relaxed alertness without any specific mental contents. Converging evidence has come from measures of metabolism, sympathetic nervous system tone and, recently, large-scale changes in gene expression. Because the exact functions of “relaxation-related” genes are not yet clear, this promising direction requires additional studies (Dusek et al., 2006; Jacobs et al., 1996).

A different procedure is called “mindfulness meditation.” Cahn and Polich (2006, 2009) describe it as “allowing any thoughts, feelings, or sensations to arise while maintaining a specific attentional stance: awareness of the phenomenal field as an attentive and nonattached observer without judgment or analysis.” Mindfulness meditation has been shown to improve depression and even suicidal thinking.

8.0 SUMMARY

Consciousness has intrigued human beings since the beginning of history. With improved scientific tools we have seen considerable progress in recent years. Attention and consciousness can be considered complementary processes (see [Figure 8.5](#)). Conscious contents often

are thought to involve the widespread distribution of focal contents, like the sight of a rabbit. As soon as we see a rabbit (consciously), we can also judge whether it's real or if it's somebody's pet. We can laugh or scream for fear of being bitten and try to remember if rabbits carry rabies. The point is that a great variety of brain events can be evoked by a conscious object, including a great variety of unconscious processes.

Conversely, we can *select* a source of information to focus on. Selective attention allows us to choose what we will be conscious of. In order to learn about the brain, we direct attention to it over and over again. Learning a difficult subject involves allocating attentional resources over time.

Consciousness typically involves a small amount of focal contents at any given moment, like the sight of coffee cup at a distance, which then may recruit and mobilize many unconscious brain functions. In attention, major functions like motivation, planning, emotional needs, and the like all interact with consciousness of a specific object in the world. Episodic and declarative types of learning seem to occur automatically as a function of conscious contents, which in turn may be guided by voluntary attention.

The three major brain states of the circadian cycle show different operating styles. A major function of slow wave sleep is to consolidate the memory of events that were initially learned in the waking state. Waking consciousness is by far the most active state in terms of survival and reproduction, the two essential activities of any species. Food seeking, infant protection, fight or flight, tracking, hunting and gathering, social interactions, mate seeking—all these goal-directed activities require the conscious state. It follows that the brain (particularly the cortex and its great input hub, the thalamus) must be able to organize itself around many different goal-directed actions during waking.

REM dreaming looks similar to waking as measured by EEG. We can remember the last 10 or 20 seconds of a dream as a conscious drama. The contents of dreams are hallucinatory, visually vivid, and often emotionally dramatic. Dream contents come from the brain itself, triggered by brainstem (PGO).

Deep sleep (slow wave sleep) appears to be unconscious, but people can remember some content when they are woken up from SWS. Slow delta waves occur at 2 to 4 Hz, and it has been suggested that we are only truly unconscious during the valleys of the slow waves, the "down" cycle of the slow wave. At those times billions of neurons pause at the same time, making it impossible for neurons to signal one another. However, SWS is not inactive. Rather, it is the best time to convert learning into permanent synaptic changes.

9.0 STUDY QUESTIONS AND DRAWING EXERCISES

9.1 Study questions

1. What brain region triggers the circadian rhythm of waking, sleep and dreaming?
2. What is the function of slow wave sleep? Of waking? Of dreaming? (If no function is established, say so.)
3. When you learn to ride a bicycle really well, what happens to your cortical activity for sensorimotor control?
4. How might two brain areas that represent the visual field be coordinated?
5. What are the physiological signs of dreaming?

6. What are the main effects of selective attention? What part of the brain appears to control voluntary, selective attention?
7. What's meant by the "architecture of sleep"? Describe its features and timing.
8. What are some hypotheses about deep or slow-wave sleep? What kind of function might it have?
9. What are the features of the conscious waking state? What kind of cortical waveforms seem to occur?
10. Describe the up state and the down state of slow-wave sleep. What are the implications for brain processing?
11. Describe neurofeedback training. What is it useful for?
12. Is there convincing evidence that hypnosis reflects a brain state?
13. What are the pros and cons of surface (scalp) EEG compared to intracranial EEG (iEEG)?
14. Meditation methods have been described for thousands of years. What are some common features? What evidence do we have pro or con?

9.2 Drawing exercise

In [Figure 8.26](#), indicate how dreams differ from waking. (Hint: What capacities are available during dreaming but not waking? During waking but not dreaming?)

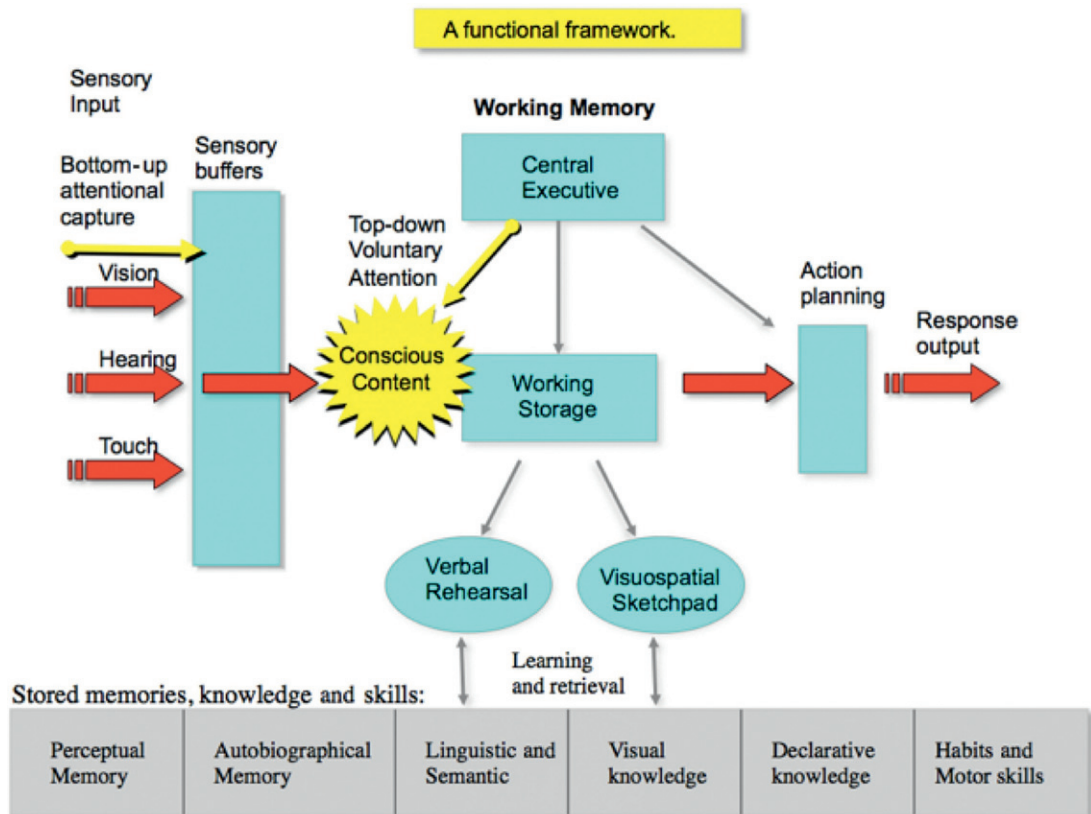


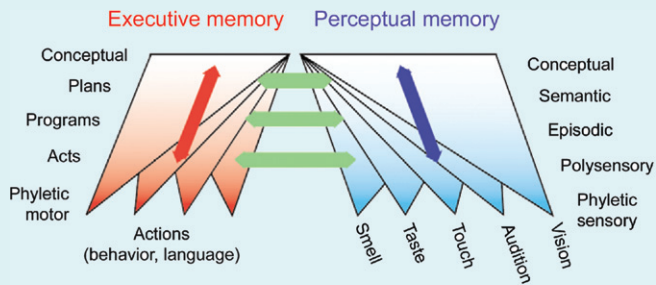
FIGURE 8.26 Source: Baars, with permission.

Learning and memory

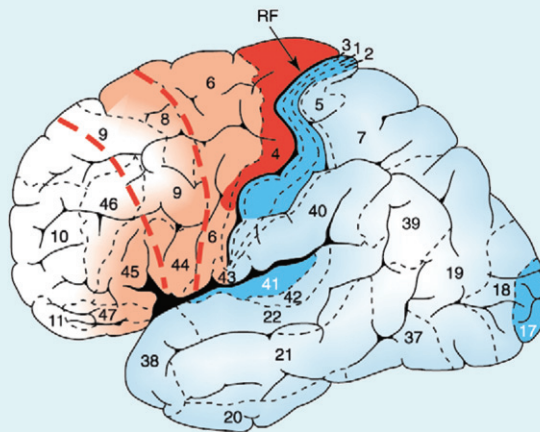
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MEMORY TRACES PERVADE THE CORTEX



(a)



(b)

Memory traces are stored in billions of synaptic links throughout the cortex and elsewhere. Because the posterior (shown in shades of blue) cortex performs perceptual functions, it also stores more perceptual memory traces. The frontal lobe (shown in shades of red) performs executive and motor roles and therefore tends to store regionally relevant memory traces as well.

Source: Fuster, 2004.

1.0 INTRODUCTION

A *memory* can be defined as a lasting brain representation that is reflected in thoughts, experiences, or behaviors. Learning is the process of acquiring such representations. Most students would like to have a “better memory,” which usually means being able to recall a large number of facts, like the ones we might need for a chemistry exam. But the human brain has not evolved for academic study and recall. Rather, it has evolved for the tasks of survival, which generally involve a lot of interaction with the things we need to know.

Our brains are adapted to deal with complex, urgent, vague, surprising, and novel life challenges, the kinds of problems that people have to solve in the real world. Perhaps for those reasons, our ability to *recognize* past events is excellent, but our ability to *recall* memories, based on partial cues, is not nearly as good. School exams are designed to test recall through partial cues, but formal schooling is a recent cultural practice. We can learn to memorize facts for recall on exams, but it takes hard work.

In contrast, learning how to throw a ball or how to recognize an old path through a forest is surprisingly easy. We can learn those things simply by paying attention (making ourselves conscious of something, as discussed in [Chapter 8](#)) and by interacting with whatever is to be learned. There is a good reason why teachers all over the world start their classes by asking students to “please pay attention.” Attention and interaction are two keys to learning.

Humans are exceptionally flexible in the face of new conditions. Our neolithic brains work well in a world of computers, brain science, and academic challenges, even though we are not biologically adapted to computers. Learning provides that remarkable flexibility.

Memory storage involves widespread synaptic strengthening among content-specific neurons in many regions of the brain (Fuster, 2004). That is why the figure at the beginning of this chapter shows that the sensory cortex appears to store sensory memory traces, while the frontal lobes store motor and executive memory traces. Memory traces are therefore *highly distributed*. We do not have a special region in the brain for storing memories.

However, the hippocampal neighborhood (the medial temporal lobe) appears to be highly specialized for converting episodic experiences into widely distributed memory traces throughout the cortex. This process occurs in stages. When we pay attention to a coffee cup on a table, our visual cortex identifies the object by way of resonant activity—the interaction of many visual “maps” that represent different features of the visual coffee cup. This activity recruits the medial temporal lobe, including the hippocampal neighborhood. This immediate memory resonance is accurate, but it is vulnerable to interference. For example, a blow to the head or an electrical shock can disrupt immediate memory.

Temporary memory resonances are converted into permanent synaptic changes during the slow wave sleep (SWS) period after learning (see [Chapter 8](#)). This process, called *consolidation*, results in protein-based brain changes that strengthen connections between active neurons. Consolidated memory traces are not easily disrupted. Synaptic strengthening seems to involve Hebbian learning, following the rule that “neurons that fire together, wire together” (see [Chapter 3](#)). That is, if two linked neurons fire at the same time, their synaptic connection will get stronger. There may be other brain mechanisms that also help to strengthen neuronal connections. The most important brain structures in this chapter are the *neocortex*—the visible outer brain—and the *medial temporal lobes* (MTL), which contain the two hippocampi ([Figure 9.1](#)).

1.1 A useful classification

Memory is not a single thing. [Figure 9.2](#) shows a standard view of known memory systems. There is ongoing research about these questions, but the terms used in [Figure 9.2](#) are important. We will focus mostly on episodic and semantic learning, which have seen a great deal of brain research. [Figure 9.2](#) starts from the top by dividing memories into two types. Declarative memory is about events and concepts, the “what, where, and when” of stored information. We are

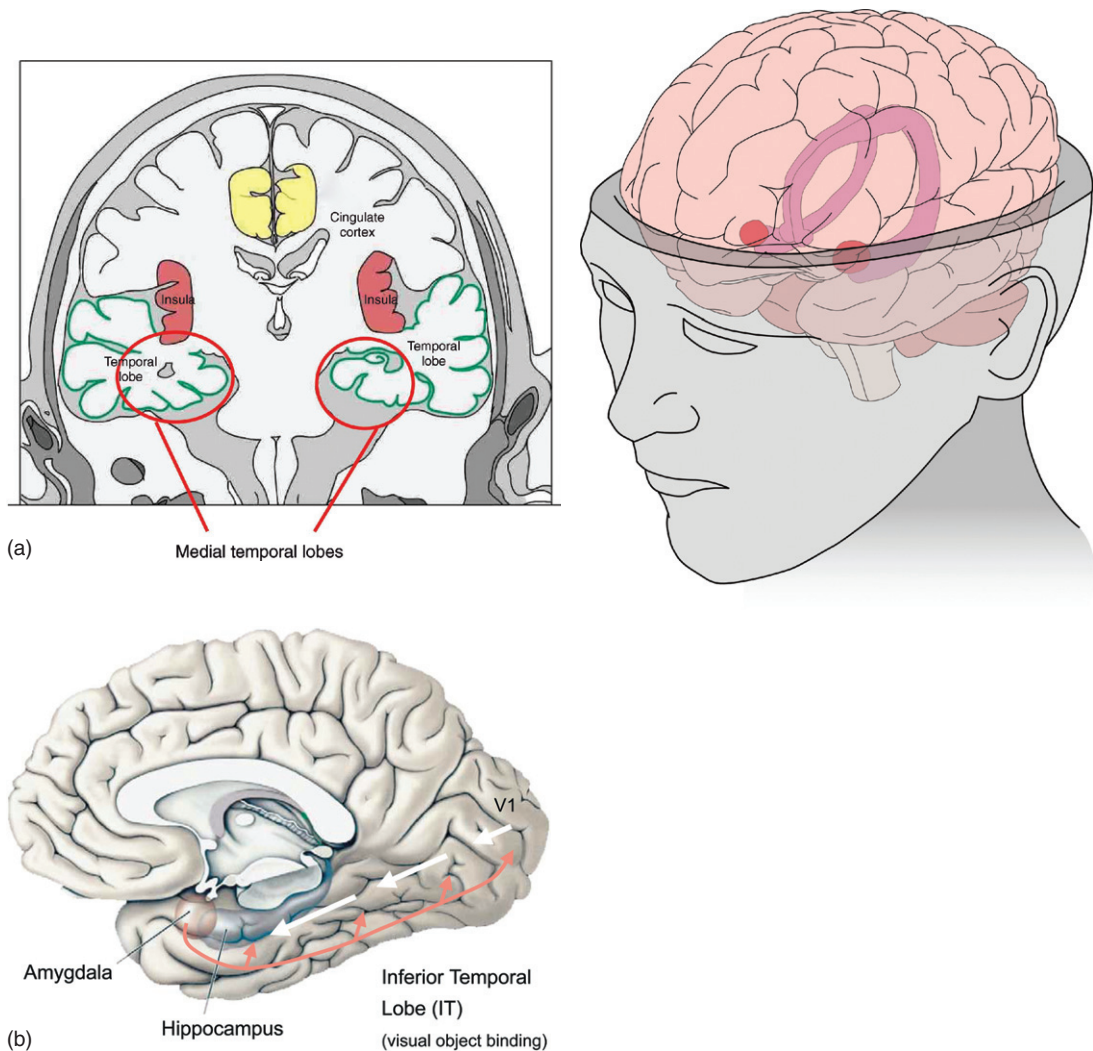


FIGURE 9.1 (a) Two views of the hippocampus: the medial temporal lobes and hippocampi. These regions are spatially complex and difficult to visualize. This figure shows two perspectives. The left panel shows a coronal section of the brain, perhaps a vertical CAT scan of the brain running between the two ears. Here we can see the hippocampi and the medial temporal lobes (MTL) circled in red. The right panel shows the three-dimensional hippocampi in both hemispheres, tipped by red structures, the amygdalae. Notice that the hippocampi are looped structures, nestled inside of each temporal lobe. The MTL includes the hippocampi and neighboring “rhinal” structures (see [Chapter 5](#)). Memory areas receive visual object information. The midline view presented in the bottom panel shows that the MTL is closely connected to area IT, the inferotemporal cortex. Area IT seems to support conscious visual object perception. The MTL also includes the amygdala. Auditory cortex is located just around the corner, on the outside of the temporal lobe. (b) The hippocampus from the midline. Source: (a) Drawn by Shawn Fu; (b) Vuilleumier, 2005.

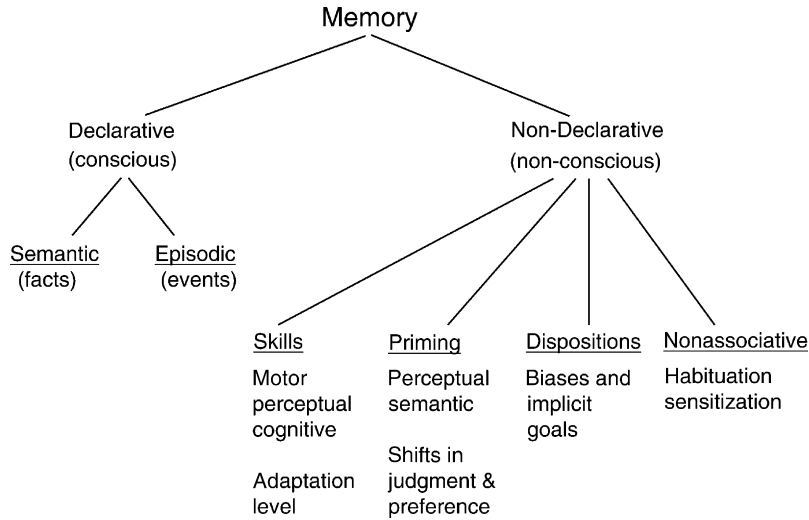


FIGURE 9.2 Schacter and Tulving proposed this classification of memory types. Declarative memories have been studied in great detail and are believed to be explicit (conscious). Nondeclarative memory types are said to be unconscious or implicit, but this claim is still debated. We will focus mainly on semantic *versus* episodic memory, where a great deal of research has been done. Source: *Squire, 2004*.

conscious of many of these “what, where, and when” properties of the world. The word *conscious* is therefore put in parentheses under the word *Declarative*. Keep in mind, however, that human beings always mix conscious and unconscious processes (see [Chapter 8](#)). One way to think about declarative memories is that we can talk about them, describe them, and point to them. That is a good behavioral index of the things we are conscious of.

Nondeclarative memory is about the “how” and “why”—knowing how to ride a bicycle, and the “why’s”—our implicit goals, tendencies, and dispositions (Banaji & Greenwald, 1995). Notice that in the diagram the word *Nondeclarative* is also called *nonconscious*. That is certainly true for many memory types in the figure.

Would you agree with these labels based on your own experiences? Remember that categories like this are helpful approximations. They are not perfect. Most of our mental activities combine several types of memory. We will focus mainly on episodic memories (memories of conscious events) and semantic memories (memories about facts and concepts).

1.2 Episodic and semantic memory

As [Figure 9.2](#) shows, declarative memory can be divided into *episodic* and *semantic memory* (Tulving, 1972). *Episodic memory* is autobiographical. It refers to memories of conscious events in our lives that have a specific source in time, space, and circumstances. We can try to travel mentally back in time to relive the original episodic experience, or something close to it. An example is your memory of what you had for breakfast today, or what happened on the day you graduated from high school. The words *episodic* and *autobiographical* are similar in meaning.

By contrast, *semantic memory* involves knowledge about the world, about ourselves, and about other people. It is often hard to remember when we learned some particular semantic memory. You may not remember when you learned that Paris is the capital of France or when you understood a new idea about the human brain. In semantic memory you don't need to remember the time and place when you learned it. All you need is a meaningful piece of information.

2.0 EPISODIC LEARNING

Episodic memories may be learned simply by paying attention to some conscious event. Episodic learning can either happen *intentionally*—when we try to learn—or *incidentally*—without deliberately trying to memorize anything. We may remember a movie scene just by paying attention to it. Paying attention may be enough to establish an episodic memory for a romantic scene at the start of a movie or the exciting chase scene at the end. If you see the same video clip years later, you may be still able to recognize it.

Human beings are extraordinarily accurate when we test for *recognition* of episodic memories, even when subjects have no deliberate intention to memorize it. That basic fact is easy to verify by checking a high school yearbook to see if you can recognize the photos of classmates you haven't seen for a long time.

The high accuracy of episodic memory *as tested by recognition measures* suggests that our brains have very large storage capacity for the things we pay attention to. Recognition measures are yes/no measures (Yes, it's familiar *versus* No, it's not). It is harder to *recall* episodic memories from partial hints (what happened on your friend's birthday five years ago?). Recall accuracy is generally lower than recognition accuracy.

Because school exams tend to use cued recall rather than recognition, it is difficult to score well on academic exams. But the effortless way in which we may score very highly on *recognition* measures suggests that a great many things we have paid attention to are “in storage” and potentially retrievable. In one classical experiment, college students were shown 10,000 pictures for six seconds each and then tested several days later, using recognition measures. They were given hundreds of “foils,” pictures they had never seen before, and an equal number of pictures they had seen before. Subjects scored above 80 percent in accuracy (Standing, 1973). No instructions were given to memorize the pictures, and six-second exposures are too brief to allow for much deliberate memorizing. Spontaneous episodic learning is therefore remarkably accurate, provided that we test for recognition rather than recall. Such evidence suggests there is much more information in memory than we usually bring to mind.

Episodic learning requires the hippocampus and its neighboring structures. A half century of brain studies have shown that the hippocampal neighborhood (the medial temporal lobe or MTL) is needed for episodic learning—converting perceptual experiences into long-lasting episodic memories. The hippocampus is shaped like a thin tube inside each temporal lobe, but many small regions in this area play special roles. For that reason the more inclusive term *medial temporal lobe* is often used.

The MTL is best seen from the bottom of the brain (see [Figure 9.1](#)). That location makes sense if you keep in mind that the hippocampus is part of the ancient olfactory brain and that the giant cortex (the neocortex) grew upward from the original brain over evolutionary epochs. In this chapter, we will refer to the cortex as the *neocortex* because we are also

discussing the MTL, which is an “older” brain region, but note that in much of this book just the word *cortex* is used to describe the neocortex.

The olfactory brain has many functions, including smell and taste. In rats (and humans) it is also involved with spatial navigation. London taxi drivers have larger hippocampi than other people, apparently because they spend years navigating through the busy and complex traffic maze of London streets (Maguire et al., 2000).

Spatial navigation is a basic need for animals, ranging from dolphins to humans. To remember a pathway through a maze or a forest, we need to store landmarks so that the next time we try to find our way through the forest, we recognize familiar places, or we might use episodic recall to imagine a shortcut across the forest. In natural surroundings survival is often dependent on path-finding, whether in nocturnal rats trying to evade a roving cat or in a dolphin navigating through the three-dimensional space of the ocean.

Humans evolved as hunter/gatherers who were mainly nomadic until 16,000 years ago. That meant a constant need to keep track of the walking clan, their children, possible enemies, sources of food, protection, shelter, and a thousand other details. For hunters and gatherers to survive, their episodic memory capacity had to be accurate.

Figure 9.3 shows our standard diagram of cognition with special emphasis on the long-term memories: the gray boxes at the bottom. Episodic events are stored in autobiographical

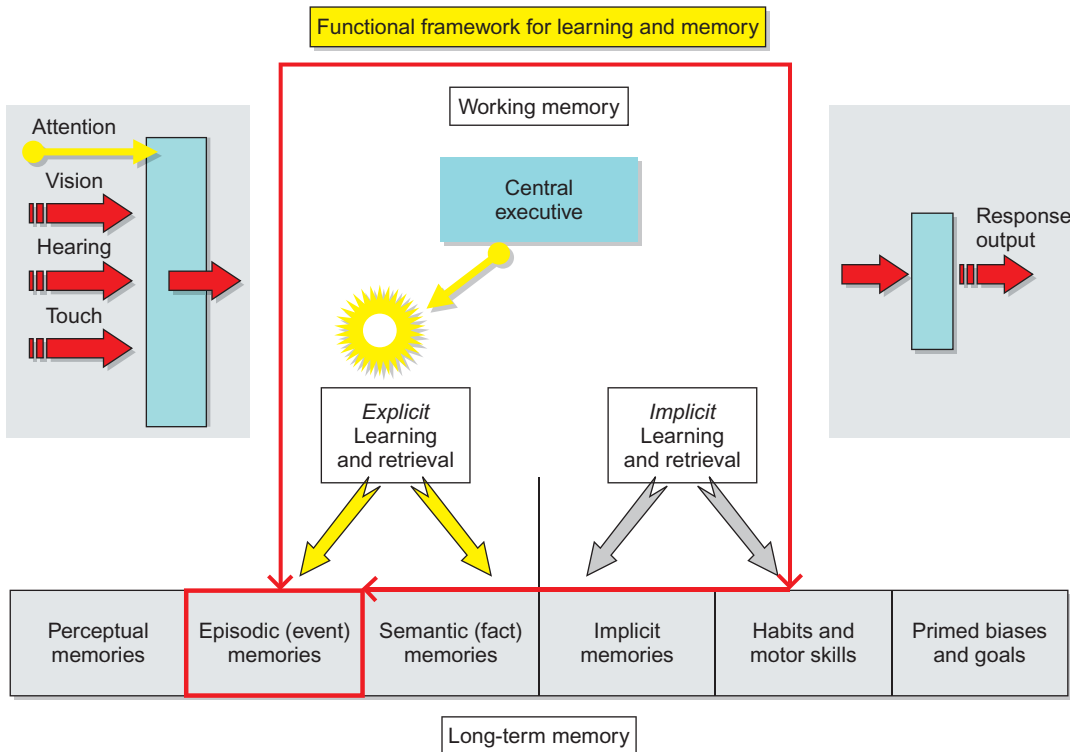


FIGURE 9.3 Episodic learning. The red arrows in this diagram trace the route of episodic information from conscious sensory input to autobiographical long-term memory. Source: Baars.

memory. The basic question in episodic learning is simply this: How do sensory and other experiences turn into long-term autobiographical memories that may be needed years later?

According to our functional diagram, when we pay attention to sensory input, it flows into *working memory*, which, in turn, allows information to be actively maintained and manipulated (see [Figure 9.3](#)). The act of paying attention tends to bring specific conscious contents to mind.

Working memory allows us to keep small amounts of information in an accessible form for 10 to 30 seconds. Many everyday tasks call upon this capacity, such as keeping a landmark in mind to find our way home in a strange city. Working memory gives us a sense of continuity by embedding our immediate conscious experiences into a psychological past, present, and future.

2.1 An example of episodic learning

Consider what happens when we first see a specific coffee cup on a table ([Figure 9.4](#)). From our chapter on vision we know that the visual brain begins by decomposing the retinal input into features in various maps in the visual hierarchy: roughly, “light points,” line orientation, size (spatial frequency), color, local motion, and ultimately shapes and textures. After the basic features are decomposed, they are “bound” together so that linked feature maps define the object: a coffee cup on a table.

While the MTL is needed to bind and transfer episodic experiences into memory, the actual memory traces are believed to be stored in the neocortex. (The word *neocortex* is often used to

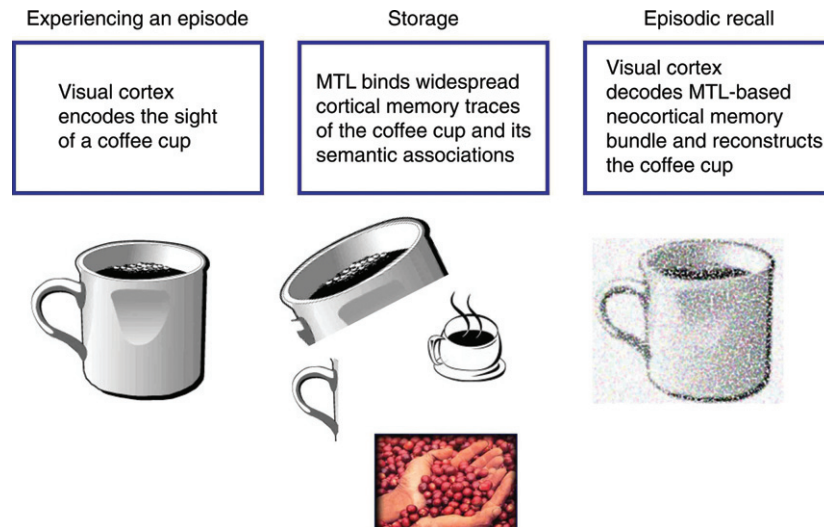


FIGURE 9.4 Episodic learning of conscious events. The sight of a specific coffee cup is encoded in visual maps for different features, like location, color, line orientation, motion, and so on. In the MTL the separate feature maps may be “bound” together into a single “gestalt.” Notice that the coffee cup is associated with a handful of raw coffee beans and with the smell of hot coffee. During slow wave sleep, the active memory of the coffee cup is recoded into lasting synaptic changes in the neocortex. Recall from episodic memory reverses these steps. Source: *Baars*, with permission.

distinguish it from the paleocortex of the hippocampus, the ancient olfactory brain. The neocortex has six layers, while the paleocortex has four or five layers.)

Memory traces must be useful in the real world, and memory *retrieval* is therefore as important as learning. When we encounter a reminder of a specific experience of the coffee cup, the bound memory traces “light up” the corresponding traces in cortex again. We thereby *reconstruct* some part of the original memory, again using the MTL to integrate memory traces into a coherent experience. That experience—of imagining the coffee cup—makes use of visual cortex again. Because this is the central theme of this chapter, we begin with a cartoon version in [Figure 9.5](#).

Visual features of the cup, like the handle, are also part of the associative complex that becomes activated. When the *episodic memory*—the sight of the coffee cup—is cued the following day—maybe by someone asking, “Did you like the way I made the coffee yesterday?”—the MTL is once again involved in retrieving and organizing widespread cortical memory traces. Visual cortex is therefore needed to reconstruct the sight of the coffee cup, which is never identical to the original cup but rather a plausible recreation of a pattern of visual activation that overlaps with the first one. Notice that visual cortex is involved in perception, learning, and episodic recall.

The difference between conscious and unconscious visual inputs is not yet fully understood. There are now many experiments on that question, and to the best of our knowledge the conscious *state* supports task-specific oscillations that combine many topographical maps to allow a single integrated bundle of activations to emerge—a “gestalt” or a whole, integrated percept.

Human subjects can report conscious events with very high accuracy, but they cannot report unconscious brain activations. Reportability has long been a useful behavioral index for conscious events. However, as we will see, there is evidence for unconscious activation of the episodic learning system as well.

Some theorists maintain that conscious gestalts are widely propagated in the corticothalamic system, including Broca’s area, which controls the vocal movements needed to verbally report conscious events (e.g., Baars, 1988; Baars et al., 2003; Connor & Shanahan, 2010; Doesburg et al., 2007; Kitzbichler et al., 2011). It is also thought that conscious events need to be represented in an

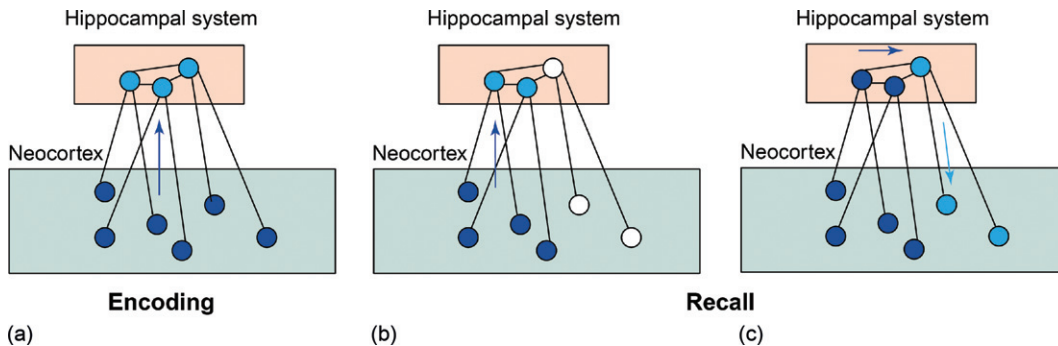


FIGURE 9.5 Hippocampus and neocortex. The hippocampal area supports temporary episodic memories that activate and are stored in the neocortex. In this cartoon, we show stages of encoding and recall and the roles of the hippocampal system and the neocortex. (a) An episodic memory is formed (Encoded) in the neocortex and gives rise to a pattern of activity with the hippocampal system. (b) During Recall, part of the pattern is active in the neocortex, reactivating part or all of the hippocampal pattern. (c) The reactivation of the hippocampal pattern will, in turn, reactivate the remaining neocortical pattern. Source: *Gluck et al., 2003*.

egocentric spatial map, an implicit “I.” In the brain such an executive network is believed to be enabled by egocentric parietal maps working together with prefrontal regions (Northoff & Panksepp, 2008). Here we will focus only on episodic encoding into long-term storage.

2.2 The medial temporal lobe

The medial temporal lobe (MTL) may be a sensory hub where visual features are “bound” into single, conscious (reportable) gestalts and widely distributed to the neocortex. During the next slow wave sleep period (SWS), the coffee cup gestalt is believed to be encoded into lasting synaptic changes throughout the cortex. In episodic recall this sequence is reversed.

Comprehending a visual stimulus like a coffee cup probably requires several hundred milliseconds. Thus in less than a second, visual cortex has identified the coffee cup in front of our eyes and triggered the MTL to bind many cortical maps to start making memory traces. However, as we will see, a permanent memory takes more time to consolidate.

The MTL is a highly interactive brain hub, well placed for integrating multiple brain regions, and for coordinating learning and retrieval from the neocortex as well. It is a “hub of hubs.” The hippocampus in the MTL is believed to be a map for spatial localization. That has been verified many times, but the hippocampus has other roles. It is associated with olfaction (smell and aspects of taste), which is why parts of the MTL are called the “rhinal,” “entorhinal,” and “perirhinal” cortex. (*Rhinos* means “nose” in Greek, as in the word *rhinoceros*, meaning “nose horn”—see [Figure 9.13](#) to find the location of the entorhinal and perirhinal cortex.

Most of the outwardly visible human brain is neocortex, which ballooned outward over evolution. The hippocampus is ideally situated to combine information between the neocortex and emotional (limbic) areas and to “bind” that information into memory traces. The large neocortex and the MTL are in constant dialogue with each other, as we store and retrieve the flow of our daily experiences.

The MTL also links with the inferior temporal lobe (see [Figure 1b](#)). You may remember that this area integrates high-level visual objects (see [Chapter 6](#)). Neurons firing in this region correlate with conscious visual perception (Sheinberg & Logothetis, 1997). Thus the MTL is strategically located to take in high-level, presumably conscious visual information. We will discuss the issue of consciousness and the hippocampus later in this chapter.

The auditory cortex is also close to the MTL, suggesting that auditory information can be fed to the episodic learning system as well (see [Chapter 7](#)). The two amygdalae are near the tips of the two hippocampi, another major hub for emotional information. Thus, the MTL is an interactive crossroad, well placed for integrating multiple brain regions and for coordinating learning and retrieval in the neocortex.

The MTL is necessary for episodic recall as well as learning. We have no way to “switch on” our MTL. Rather, we simply pay attention to whatever we want to remember. In most cases that means that we become conscious of the material to be learned, and episodic learning seems to happen with no intention to learn.

The episodic memory trace consists of an ensemble of the MTL and neocortical neurons, while the MTL acts as a pointer to the neural elements in neocortex for the event. Retrieval occurs when a conscious cue triggers the MTL, which in turn activates the entire neocortical ensemble associated with it. When we recover episodic memories, we bring to mind

something close to the original conscious experience (Moscovitch, 1995). The recovery of these experiences always depends on the hippocampus. As Moscovitch (1992) has argued, the hippocampal complex acts as a module whose domain is consciously apprehended information.

Some recent studies, however, have questioned this hypothesis. Using fMRI, Henke and her collaborators (2003; see also Degonda et al., 2005) showed that the hippocampus can be activated by subliminal presentation of faces and their associated professions. Moreover, these activations are correlated with performance on subsequent explicit tests of memory for faces-profession pairs. Likewise, Daselaar and colleagues (2006) found that the posterior MTL was activated more by old, studied items at retrieval, even when the person was not aware that the item was old. Finally, Schendan and colleagues (2003) showed that the hippocampus was activated on a similar memory task if the repeated sequences were of a higher order of association.

There also have been similar reports from studies with amnesic patients. Ostergaard (1987) was the first to suggest that performance on some priming tests was related to the extent of medial temporal damage. More recently, Chun and Phelps (1999) showed that nonconscious context effects in visual search were not found in amnesic patients, suggesting that the MTL was needed for retaining contextual information of which the person was not aware. Likewise, Ryan et al. (2000) showed that amnesic people did not show the normal pattern of eye movements around the location where a change occurred in a studied picture, even though neither they nor the normal controls were consciously aware of the change. Thus the role of the hippocampus does not seem to be limited to consciously apprehended information, as proposed by Moscovitch (1992).

2.3 Multiple traces in the cortex

Nadel and Moscovitch (1997) proposed a *multiple trace theory*, suggesting that the hippocampal complex rapidly encodes all information that becomes conscious. The MTL binds the neocortical neurons that represent the conscious experience into a memory trace. The MTL neurons act as a pointer, or *index*, to the neocortical ensemble of neurons that represent the experience (Teyler & DiScenna, 1986). A memory trace of an episode, therefore, consists of a bound ensemble of neocortical *and* MTL neurons. Formation of these traces is relatively rapid, lasting on the order of seconds or at most days (Moscovitch, 1995).

In this model, there is no prolonged consolidation process that slowly strengthens the neocortical memory trace. Instead, each time an old memory is retrieved, a new hippocampally mediated trace is created, so that old memories are represented by more traces than new ones and therefore are less susceptible to disruption. Because the memory trace is distributed in the MTL, the extent and severity of retrograde amnesia is related to the amount and location of damage to the MTL (Figure 9.6).

While each autobiographical memory trace is unique, the existence of many related traces facilitates retrieval. Episodic memories are integrated to form semantic memories. Thus facts about people and events that are learned in specific episodes become separated from their sources. This process may give the appearance of classical consolidation, but the brain mechanism is different from the classical view.

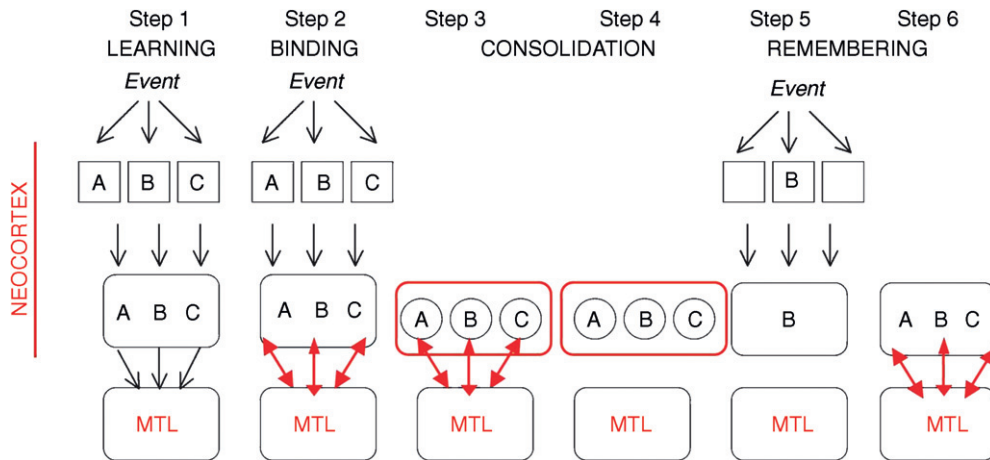


FIGURE 9.6 The steps of learning, binding, consolidation, and remembering. In this summary, Step 1 is the learning of an event, consisting of three elements, A, B, and C. It is initially encoded by the neocortex (such as the visual cortex) and sent to the MTL. In Step 2, the MTL and the neocortex resonate with each other to begin establishing the memory trace. In Step 3, the stimulus event is no longer available, and the MTL-neocortical resonance is now independent of external support. Step 4 shows how consolidation leads to permanent, separate memory traces (synaptic changes) in both the MTL and the neocortex, which now exist separately from each other, while other input is being processed. In Step 5, element B of the original event (A-B-C) is presented as a reminder or recall cue. In Step 6, the memory traces of A-B-C are activated by resonating activity between the MTL and the neocortex. At this point, the episodic memory has been retrieved in the absence of the original stimulus. Source: *Moscovitch, modified with permission.*

As we will see, the “central executive” of working memory plays a role in long-term learning and retrieval. For example, if you are trying to learn a word, you might deliberately rehearse it to yourself, using your executive capacities to control inner rehearsal and to shut out distractions. When you are studying for a test, it is a good idea to monitor your own performance “metacognitively”—that is, to think about your own thinking process and to see if your understanding of the material is good enough to pass the exam. All these are examples of executive processes (see [Chapters 10, 11, and 12](#)).

However, more permanent memories are believed to require protein synthesis—such as the growth of dendritic spikes, tiny stalks that grow on top of axons and dendrites, bearing new synaptic connections with neighboring neurons.

2.4 “Excitatory” and “inhibitory” memory traces

Most synapses in the cortex are excitatory, using the neurotransmitter *glutamate* (see [Chapter 3](#)). A very large minority use inhibitory neurotransmitters like *GABA* (gamma-aminobutyric acid). To encode long-term memory traces in changed synaptic efficiency, these excitatory and inhibitory connections must somehow be made more permanent. These two processes are believed to occur in what is called long-term potentiation (LTP) for excitatory synapses and long-term depression (LTD) for inhibitory ones. These events, which have been observed in specific regions, are simply an increase and a decrease in the firing probability of a postsynaptic potential given a presynaptic spike.

LTP has been observed in the hippocampus, using single-cell recording in one of the neuronal layers of the hippocampus. Single-cell recording has been extensively done in animals, but there are cases of such recordings in human epileptic patients as well (Kreiman et al., 2002). While we can observe LTP and LTD in specific locations like the hippocampus, the standard hypothesis about long-term memory involves billions of synapses in cortex and its satellites, amounting to literally trillions of synapses. We have no way of taking a census of all of the synapses in this system, or even a substantial fraction of them, at this time. Rather, we have a number of studies showing increased LTP and LTD, supplemented by studies of brain damage and of population activity among billions of neurons as measured by EEG, ERP, fMRI, and so on. In addition, we have evidence from stimulation studies, like temporal lobe stimulation of awake patients during neurosurgery and transcranial magnetic stimulation (TMS) in normal subjects. What we know about memory is therefore an inferential picture, in which many hundreds of studies have been performed. But we cannot yet come close to observing large numbers of changed synaptic connectivities directly at the submicroscopic level.

Our current picture suggests these points:

1. Episodic input is initially analyzed by the neocortex.
2. It is integrated for memory purposes in the MTL, containing the hippocampi and related structures.
3. Consolidation: MTL and related regions then bind and integrate a number of neocortical regions, a process that transforms temporary synaptic connectivities into longer-lasting memory traces in both the MTL and neocortex. The main mechanisms for such changes are believed to be LTP and LTD.

2.5 Theta rhythms coordinate hippocampus with cortex

[Chapter 8](#) pointed out two basic coding mechanisms in the brain. First, there are numerous linked maps, like the topographical arrays of the visual system. These arrays or “maps” are linked to one another by the axons sprouting from each cell. Linked spatial arrays provide a kind of spatial code for the brain. In addition, the brain uses neural spiking and population oscillations to allow active communication between its large collection of flat cellular arrays. For example, communication between the MTL and the neocortex seems to involve theta rhythms (4–7 Hz). Theta rhythms appear in the frontal lobes during episodic memory retrieval. Depth electrodes placed in the hippocampi show the same results (Siapas et al., 2005). [Figure 9.7](#) shows how theta rhythms may emerge from neurons firing in synchrony in the theta frequency range and adding up their activities to cause smooth population waves.

3.0 MAKING MEMORIES LAST

3.1 Consolidating traces in the cortex

We can now add the final steps. [Chapter 2](#) suggested a widely accepted hypothesis about the relationship between immediate memory and long-term memory called the *consolidation hypothesis*. Consolidation is generally defined as a progressive stabilization of long-term

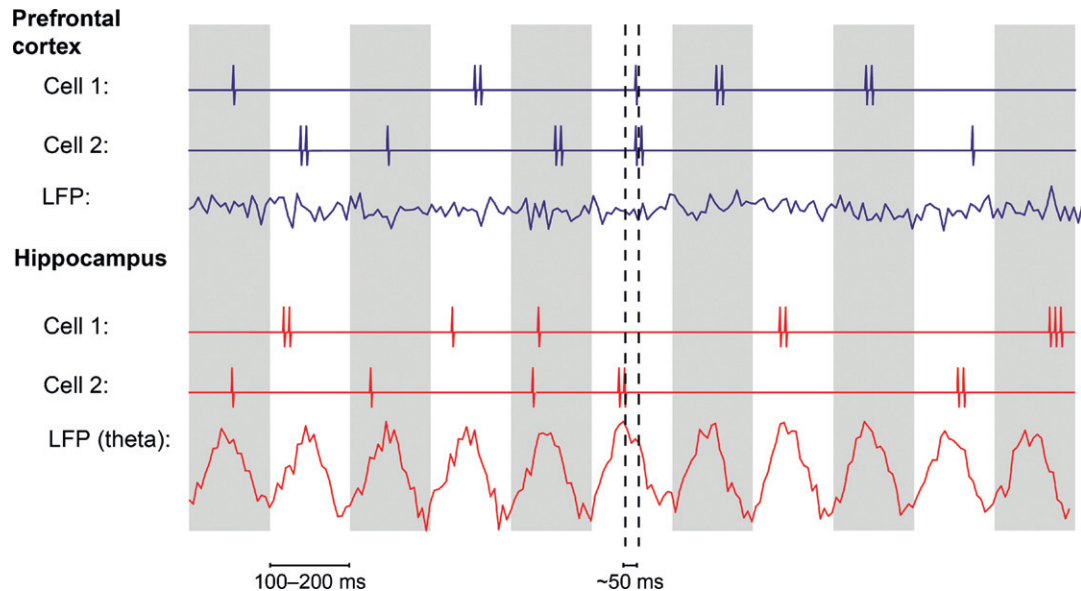


FIGURE 9.7 Theta rhythms from neural firing. It is widely believed that regular oscillations are used to “bind” different neural “maps” to each other. In communicating between the MTL and the neocortex, it is believed that theta oscillations play that role. Other, faster oscillations may ride on top of theta waves. This figure suggests how synchronous firing in neurons can add up to theta oscillations in small populations of neurons. (LFP stands for “local field potential,” the recording of a local electrical field by electrodes placed outside of neurons.) Source: *Jensen, 2005*.

memory traces so that they are relatively resistant to decay or disruption. (But recall Nadel and Moskovich’s theory.) It is this process that is absent or severely disrupted in amnesic patients and accounts for their poor ability to transfer information from short- to long-term memory.

3.2 Rapid consolidation: synaptic mechanisms, gene transcription, and protein synthesis

Rapid or synaptic consolidation is accomplished within the first minutes to hours after learning occurs. Weiler and colleagues (1995) showed that it correlates with morphological changes in the synapse itself. Stimulus presentation initiates a cascade of neurochemical events at the synaptic membrane and within the cell, which increase the synaptic strength or efficiency with which neurons that form the memory trace can communicate with one another. The first of these processes involves local, transient molecular modifications that lead to an increase in neurotransmitter release at the affected synapse. If the stimulus is intense enough and/or repeated, additional processes are activated. These involve gene transcription and protein formation that lead to long-lasting cellular changes, including the creation of new synapses that support the formation and maintenance of long-term memory (Figure 9.8). These processes may last from hours to days (Dudai, 2004; Lees et al., 2000; McGaugh, 2000).

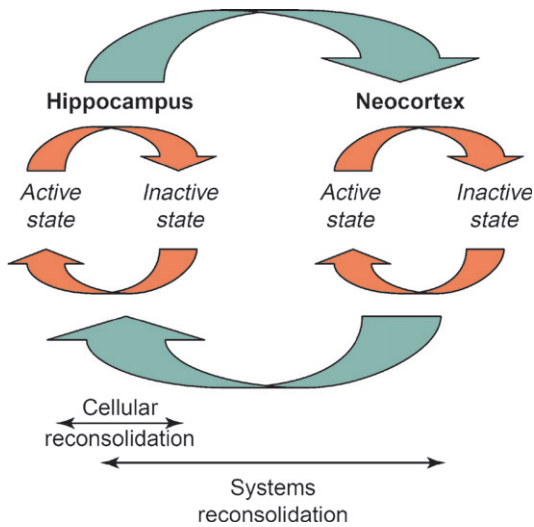


FIGURE 9.8 Consolidation turns active neuronal connections into lasting ones. Two kinds of consolidation are believed to exist: cellular and systems consolidation. Both are evoked by activation of the MTL and neocortex. This diagram emphasizes the degree to which the MTL (also called the hippocampal complex) and the neocortex establish active cell assemblies corresponding to the learned input, in which neurons resonate with each other until more permanent connections are established. Source: *Nader, 2003*.

Though we are well on our way to understanding the basic cellular and molecular mechanisms of synaptic consolidation, we are far from understanding prolonged or system consolidation, which is being debated heatedly in the literature.

3.3 System consolidation: interaction between the medial temporal lobes and the neocortex

System consolidation can take much longer to complete and may range from days to years or decades. Patients with MTL lesions show a retrograde memory loss that is temporally graded, so recent memory loss (before the amnesia) is greater than earlier memory loss. This temporal gradient is restricted to explicit memory, leaving implicit memory intact and stable over time (Scoville & Milner, 1957).

These observations suggest that the MTL forms a temporary memory trace needed for explicit memories until they are consolidated elsewhere in the brain, presumably in the neocortex (Squire, 1992; Squire & Alvarez, 1995). This standard model of consolidation makes no distinction between various types of explicit memory. For instance, it predicts a similar pattern for episodic and semantic memory.

Nadel and Moscovitch (1997, 1998) concluded, contrary to the standard consolidation model, that the MTL is needed to represent even old episodic memories for as long as the memory exists (Moscovitch & Nadel, 1998; Nadel et al., 2000). The neocortex, on the other hand, is sufficient to represent *repeated* experiences with words, objects, people, and environments. The MTL may aid in the initial formation of these neocortical traces, but once formed they can exist on their own. Thus unique autobiographical memories are different from repeated memories in that they continue to require the MTL. Repeated experiences are proposed to create multiple traces, adding more traces each time the event is brought to mind.

Neuroimaging studies provide evidence for this interpretation. These studies found that the hippocampus is activated equally during retrieval of recent and remote autobiographical

memories (Conway et al., 1999; Gilboa et al., 2004; Ryan et al., 2000; for review, see Maguire et al., 2000; Moscovitch et al., 2005, 2006). These questions continue to be debated at this time.

The prefrontal cortex (PFC) plays a role in working memory. The prefrontal cortex is situated in front of the motor cortex in both humans and other primates (Figure 9.9). The macaque monkey has been the primary experimental animal in many studies of working memory. Obviously, humans have other abilities, like language, that are not directly paralleled in other species. But in the case of working memory studies, the macaque has been a constantly important source of evidence.

Knowledge of a link between the PFC and short-term memory dates back to the 1930s, when it was first discovered that large bilateral lesions of the PFC in animals impaired performance on a delayed response task. In this task, a sample stimulus is presented (e.g., a color or location), and its identity must be maintained over a short delay period so it can guide a later response (Figure 9.10). Using variants of this basic task with more recent neuroscientific

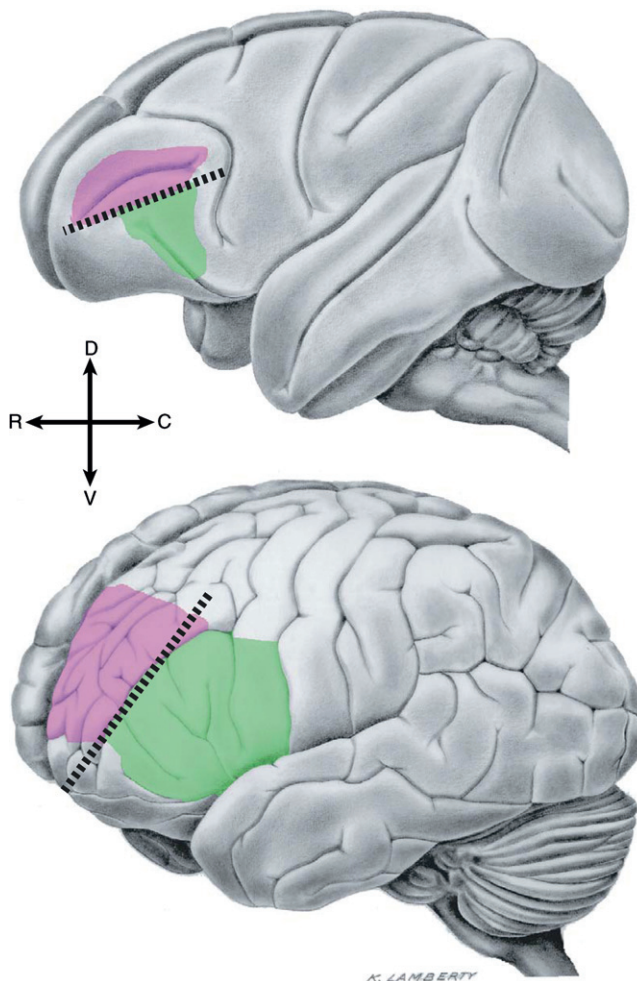


FIGURE 9.9 The prefrontal cortex in monkeys (top) and humans (bottom). The most common division is between the upper and lower halves of the prefrontal cortex (PFC), called the dorsolateral prefrontal cortex (DL-PFC) for the light purple region and the ventrolateral prefrontal cortex (VL-PFC) for the light green area. Also notice the orientation cross, pointing to dorsal (upper), ventral (lower), rostral (toward the nose in humans), and caudal (toward the back of the head in humans). Source: Ranganath, 2006.

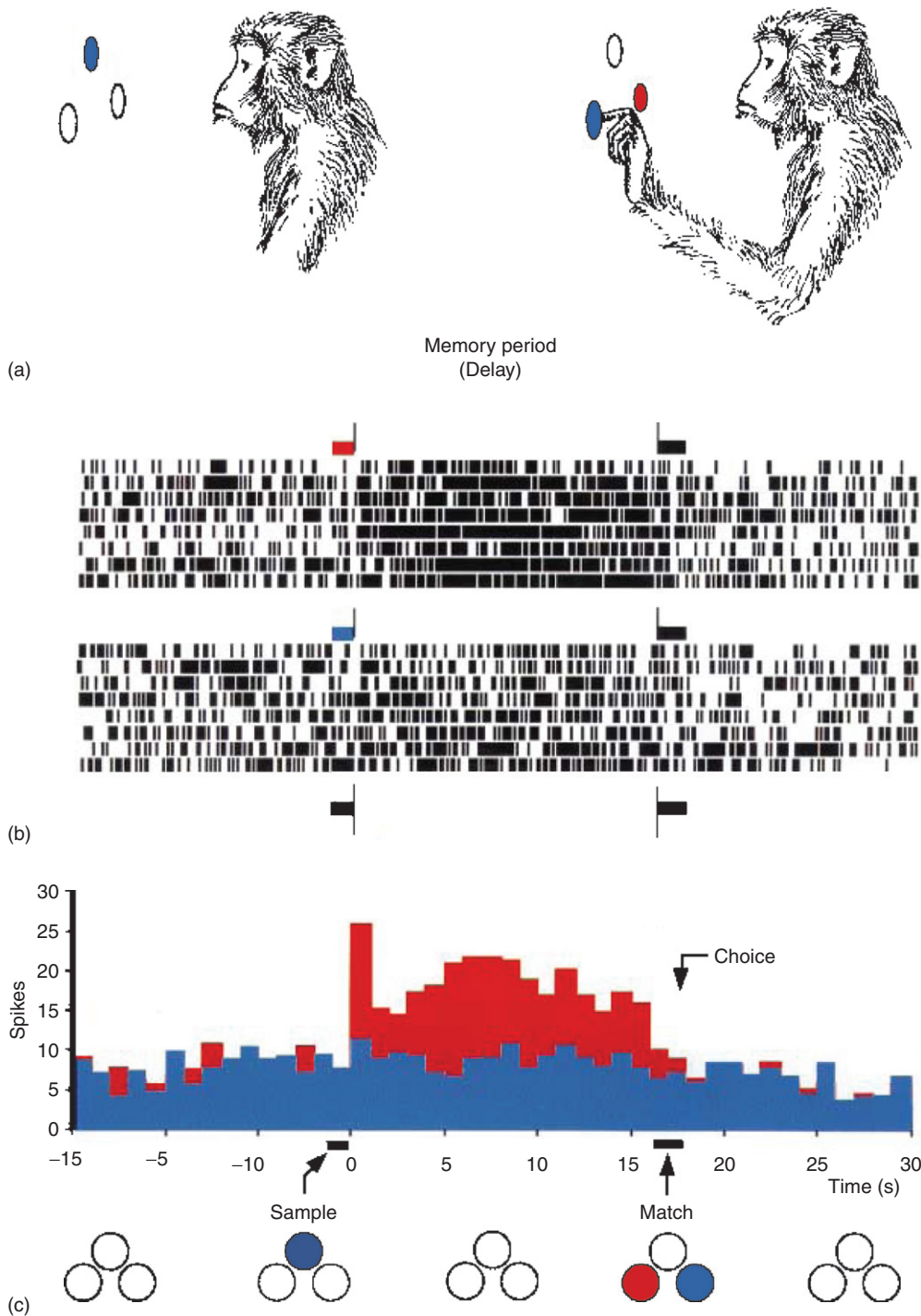


FIGURE 9.10 “Delayed match to sample (DMTS)” in the macaque. In a classic experiment, a macaque monkey is trained to delay responding to a stimulus—in this case the location of a red, white, or blue light. The monkey shows recognition of the stimulus after delay by matching it in the display in a task called “delayed match to sample.” In effect, the monkey is communicating “This is what I saw.” DMTS methods are widely used in animals, nonverbal babies, and other subjects. Source: *Fuster, 1997*.

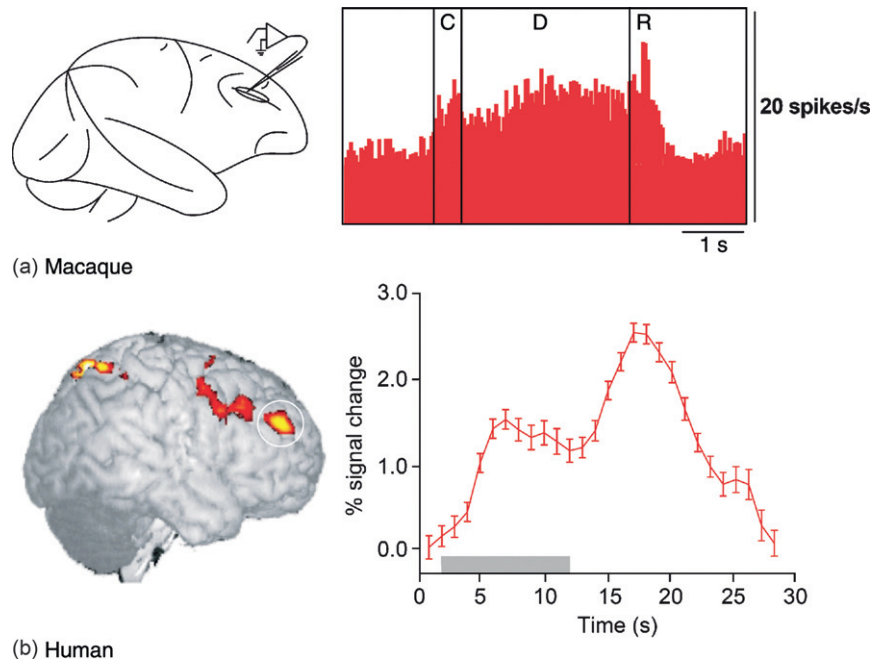


FIGURE 9.11 A delayed-response task to study working memory in monkeys and humans. It has been proposed that the PFC serves a specific role in the active *storage* of information in working memory (e.g., Goldman-Rakic, 1998). That is, sustained activity in prefrontal neurons reflects this region's role in maintaining specific representations of the items that must be kept in mind over the delay. This interpretation is supported by the finding that individual neurons in the PFC are selective for particular target stimuli. For example, a given cell may fire strongly over the delay period when the target is in the upper left portion of the display but weakly when the target is elsewhere in the display. This pattern suggests direct involvement in the internal representation of target features. In this figure, neurons in prefrontal cortex respond during the delay period in a delayed-match-to-sample task. Results in macaques (a) and humans (b) are similar. Source: Curtis & D'Esposito, 2003.

techniques, modern research has firmly established the role of the PFC in active maintenance of WM information (Figure 9.11).

Much of the animal research has focused on a specific frontal region called the dorsolateral prefrontal cortex (DL-PFC; see Figure 9.9). (In the human cortex, *dorsal* is “upper” and *lateral* means “to the side.”) One of the key early findings came from the laboratory of Joaquin Fuster (Fuster & Alexander, 1971). Fuster and his colleagues trained monkeys to perform a delayed-response task in which the monkeys had to remember a color over a brief delay and then point to the correct color when later presented with two alternatives. Since no information about the correct color was offered after the initial presentation, its identity had to be retained in working memory. Using implanted electrodes to record neural activity during performance of the task (see Chapter 4), it was found that individual neurons in the monkey DL-PFC exhibited sustained and persistent activity across the delay period. That is, after the color had been removed from the visual display, neurons in the DL-PFC continued to fire at an increased

rate, and this activity then subsided once the match/nonmatch response was made (see [Figure 9.10](#)).

This pattern of sustained delay-period activity in the DL-PFC has been replicated many times since, and in a wide variety of tasks. For example, to confirm that PFC contributions are truly memory-related and not simply a reflection of subtle preparatory motor gestures, Patricia Goldman-Rakic and her colleagues developed a version of the task in which monkeys see a target presented briefly at one of several possible locations on a display and then, after a delay, must shift their gaze to that location in order to receive a reward (see Levy & Goldman-Rakic, 2000, for a review). Importantly, the monkey is required to look straight ahead until the end of the delay period, so neural activity during the delay cannot be simply a by-product of moving the eye but must instead reflect memory processes. Again, this paradigm produces sustained neuronal activity in the DL-PFC and, what's more, the *amount* of delay-period activity predicts whether or not items will be remembered; when DL-PFC delay-period activity is weak, there is a greater likelihood of forgetting (Funahashi et al., 1993).

There is some debate about whether PFC is subdivided according to the content of the information that is stored or according to the function that each region carries out. According to the content approach, the DL-PFC seems to be particularly involved in holding onto information about spatial locations, whereas different parts of the ventral and lateral PFC have been implicated in storing nonspatial types of information (e.g., objects, faces, words, etc.). Alternatively, each of these regions may have different functions, with DL-PFC implicated in manipulation of information and VL-PFC in maintenance (ventro-lateral—downward and to the side). The term *ventral* refers to the down direction in cortex; literally, *ventrum* means “belly” in Latin.

Monkey brain lesion studies have further implicated the PFC, and the DL-PFC in particular, in working memory function. With very precise techniques for localizing experimentally induced lesions, it has been shown that damage isolated specifically to the DL-PFC is sufficient to impair performance on working memory tasks (Fuster, 1997). Such findings show a causal role for the PFC in working memory. Not only are cells in this region active during a delay, but their lesioning impairs working memory. This impairment gets worse as the length of the delay increases, suggesting that there is more rapid forgetting when the PFC is prevented from sustaining them.

Studies in humans using neuroimaging have corroborated many of the findings from the animal literature. Hundreds of imaging studies have shown PFC activity when participants are trying to maintain task-relevant information. Consistent with the animal work, fMRI studies in humans show that PFC activity persists during the delay period of a working memory task (see [Chapters 5, 10, and 12](#)).

Human neuroimaging studies have also varied *working memory load*—the number of items that must be held in immediate memory (Cohen et al., 1997; Rypma et al., 2002). In one study, memory load was varied between one and eight items, and subjects had to hold these items for a short delay. PFC activation was found to be positively correlated with the number of items in memory. Such “load dependence” in the PFC supports the notion that this part of the brain is involved in working memory storage (see [Chapter 12](#)).

While PFC contributions to working memory have been clearly demonstrated, its specific contribution to working memory storage has been recently questioned. Several other cortical and subcortical areas exhibit similarly persistent stimulus-specific activity over short

delays. It appears that PFC may be part of a more distributed brain network supporting working memory. Other data suggest that the PFC may not be involved in storage per se but in providing top-down, or *executive*, support to other regions where information is actually stored.

4.0 WHEN MEMORIES ARE LOST

4.1 Hippocampal versus cortical damage

[Chapter 2](#) touched on the case of Clive Wearing, who has lived with a dense amnesia since 1985, when a viral infection destroyed some brain areas for memory. Over a few days, Wearing was transformed from a rising young musician to a man for whom each waking moment feels like the first, with almost no recollection of the past and no ability to learn for the future.

Little has changed for Wearing since 1985. While he cannot recall a single specific event, some aspects of his memory are spared. He can carry on a normal, intelligent conversation. Some short-term memory is spared, allowing him to stay with a topic over several seconds. He has retained general world knowledge, an extensive vocabulary, and a tacit understanding of social conventions. Wearing also remains a skilled musician, able to play complex piano pieces from sheet music. Though he cannot remember specific events, he does recall a limited number of general facts about his life. Among the few memories that have survived is the identity of his wife, Deborah. He greets her joyfully every time she comes into his room, as though they have not met for years.

However, just moments after she leaves, Clive Wearing cannot remember that she was there at all. In a recent book, Deborah Wearing (2005) tells of coming home after visiting Clive at his care facility and finding these messages on her answering machine:

Hello, love, 'tis me, Clive. It's five minutes past four, and I don't know what's going on here. I'm awake for the first time and I haven't spoken to anyone. . . .

Darling? Hello, it's me, Clive. It's a quarter past four, and I'm awake now for the first time. It all just happened a minute ago, and I want to see you. . . .

Darling? It's me, Clive, and it's 18 minutes past four, and I'm awake. My eyes have just come on about a minute ago. I haven't spoken to anyone yet, and I just want to speak to you.

Wearing's history suggests that amnesia is selective—certain kinds of memory may survive, while others are lost. Learned skills, like the ability to speak or play the piano, are different from episodic memories. Thus memory is not unitary but consists of different types.

Amnesic memory loss varies in degree. Clive Wearing's amnesia resembles that of other patients, but he is unusual in his nagging sense that he has just awoken from some unconscious state. He also "perseverates," repeating the same thoughts and actions over and over again, as in the repetitive telephone messages he leaves for his wife. These symptoms may result from additional damage to prefrontal structures that allow us to monitor our own actions.

Another patient, known as HM, is by far the best-studied victim of amnesia. In the case of HM we know exactly where the lesion occurred ([Figures 9.12](#) and [9.13](#)). This makes him very rare. Most brain injuries are very "messy," can spread wider than the visible lesions, and may

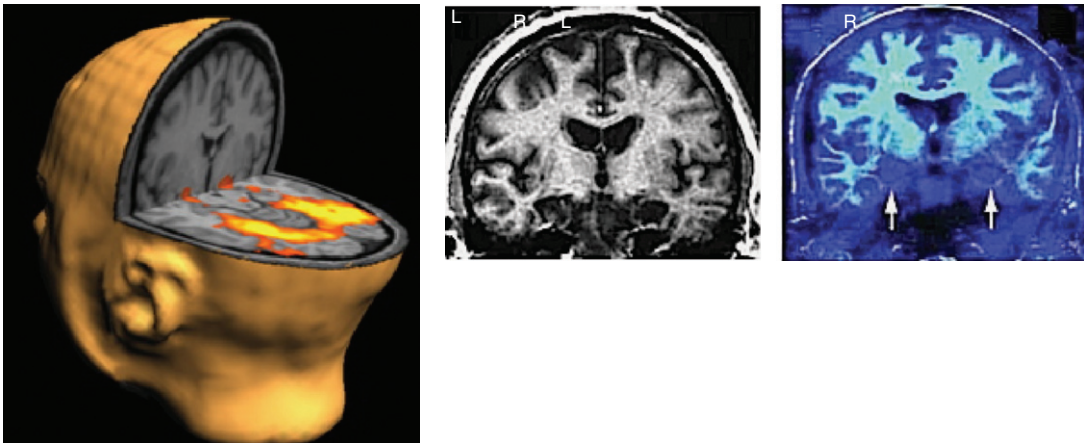


FIGURE 9.12 Lost brain tissue in the case of HM. The two arrows in the blue cross-section of the brain point to lost tissue in the hippocampus on both sides (hemispheres). The gray photo shows actual black regions where the tissue was lost. Sources: Left: *Aminoff & Daroff, 2003*; right: *Corkin et al., 1997*.

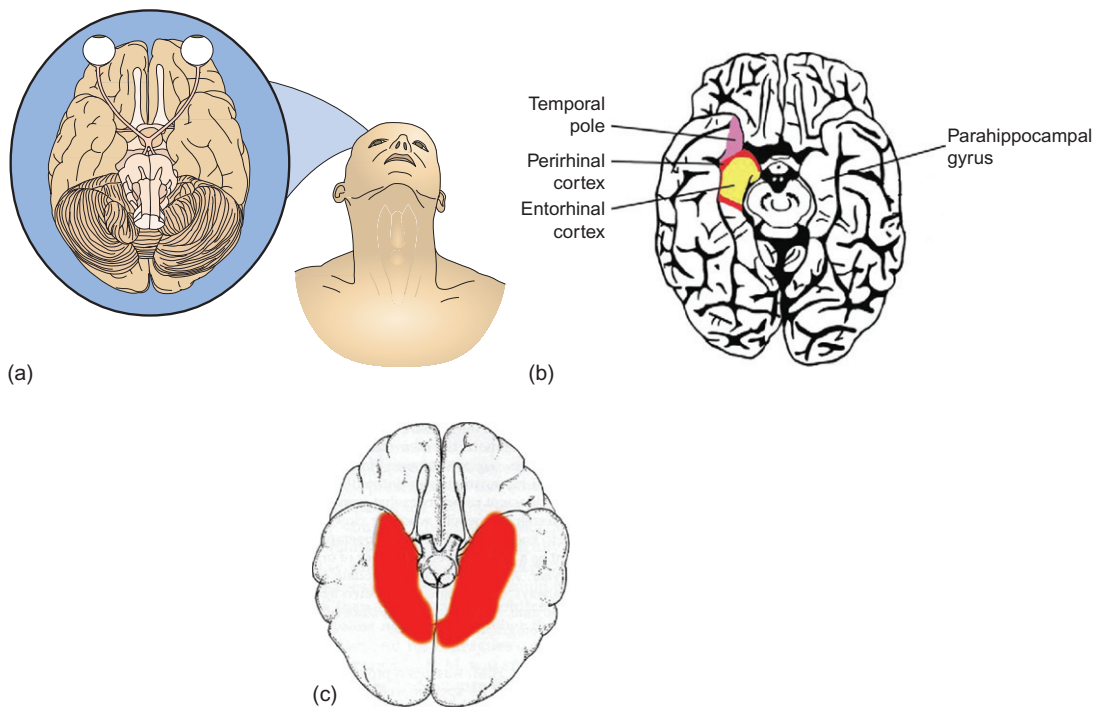


FIGURE 9.13 HM: Surgically removed MTL. The medial temporal lobes and HM's lesions, seen from below. (a) The orientation of the head and brain; (b) the bottom of the MTL, with major subregions for memory labeled. Notice that the rhinal (smell) cortices indicate the ancient origin of this region. In all figures you can see the two olfactory bulbs pointing upward, an important landmark for orientation. (c) The surgical lesion in HM's brain. The surgeon at the time was unaware of the importance of this region for memory. Source: (a) *Baars & Fu, with permission*, (b) *Buckley & Gaffan, 2006*; (c) *Moscovitch, personal communication*.

change over time. Clive Wearing's viral infection apparently destroyed hippocampal regions on both sides of the brain but also some frontal lobe areas. Wearing may also have suffered brain damage that we simply do not know about. In the case of HM, however, because his lesion was carefully performed by a surgeon, we know that both sides of the MTL were removed as accurately as was possible at the time. The extent of HM's brain damage and functional deficits has been verified with great care in more than 100 published articles. This has made HM one of the most important patients in the history of brain science (Box 9.1).

4.2 Defining amnesia

Amnesia is any major loss of memory while other mental functions are still working. The cause can be infection, stroke, tumor, drugs, oxygen loss, epilepsy, and Alzheimer's disease. Amnesia can also be *psychogenic*, resulting from trauma or hypnotic suggestion (Nilsson & Markowitsch, 1999).

As we have seen, amnesia can be caused by bilateral damage to the medial temporal lobes, which includes the hippocampal formation. While explicit memories are impaired, there are surviving functions:

1. Perception, cognition, intelligence, and action
2. Sometimes working memory is spared
3. Remote memories
4. Implicit memory

As mentioned, implicit memory is commonly assessed by priming tasks. Perceptual priming is mediated by sensory cortex, and conceptual priming is believed to involve both the temporal and prefrontal regions. Amnesics do not lose their capacity to perform well on priming tasks, such as word-fragment completion. For example, subjects may study a list of words (such as *metal*) and are tested with fragments of the words they studied to see if they can complete them (*met__*). The study phase increases the speed of completion. On such tasks, amnesic patients can perform as well as normals.

Functional neuroimaging studies confirm the perceptual locus of perceptual priming. Unlike tests of explicit memory, which are associated with *increased activation* during retrieval in regions that support memory performance, such as the MTL and the prefrontal cortex, perceptual priming is associated with *decreased activation* on repeated presentations in regions believed to mediate perceptual representations. Thus repeated presentation of faces and words leads to decreases in activation in inferior temporal and extrastriate cortex which mediate face and word perception (Schacter et al., 2004; Wigg & Martin, 1998).

In conceptual priming the relationship between study and test items is meaning-based. Conceptual tasks include word association ("Tell me the first word that comes to mind for *elephant*"), category exemplar generation ("Provide examples of animals"), and general knowledge ("What animal is used to carry heavy loads in India?") (Moscovitch et al., 1993; Roediger & McDermott, 1993). Conceptual priming occurs if studied words (e.g.,

BOX 9.1

THE CASE OF HM

The science of memory received a major boost from Herbert Scoville and Brenda Milner's (1957) report of a memory disorder in HM after bilateral removal of his medial temporal lobes to control severe epileptic seizures. As a result of a head injury from a bicycle collision when he was a young boy, HM was beset with epileptic fits that increased in frequency and severity into his late 20s. As a treatment of last resort, Scoville performed an operation in which he removed tissue in and around the hippocampus on both sides of HM's brain (see [Figure 9.12](#)). While the surgery reduced HM's seizures, it had a profound and unexpected impact on his memory. This result was unknown at the time, and Scoville would undoubtedly have changed the procedure had he known about this harmful result. The report of HM's case by Scoville and Brenda Milner was the first to demonstrate directly the importance of the hippocampus and surrounding structures for memory.

As a result of the operation, HM could not remember any of the events of his life thereafter—the people he met, the things he did, events taking place in the world around him. As an adult, he could not keep track of his age and could no longer recognize himself in the mirror because he was unfamiliar with his changed appearance. In addition to this *anterograde* (postdamage) memory deficit, HM also could not remember events or experiences from the years immediately before the surgery, a *retrograde* amnesia. While his episodic (autobiographical) memory loss was acute, other cognitive functions seemed to

be intact. He could reason, solve problems, and carry on a normal conversation. His intelligence was normal, and he retained his language abilities.

HM had intact short-term memory. He performed like healthy controls on tests of working memory, such as the digit span task. HM had been under the care of doctors from a young age, and his intellectual abilities before surgery were well documented. The specific locus of damaged tissue was both limited and well characterized. In most amnesias, the damage is more widespread and difficult to identify. HM had been tested and imaged a number of times since his surgery, giving a very complete picture of his condition.

As you can tell from [Figures 9.12](#) and [9.13](#), HM had an apparently intact neocortex—the outer structures in brain scan. Like Clive Wearing, HM could carry on a normal conversation. He could discuss the immediate present, using his general knowledge of the world. He was conscious, had normal voluntary control over his actions, and appeared to be emotionally well adjusted. It was only when his episodic memory was tested that he revealed that he simply could not remember the past or learn new memories for the future.

It is useful for you to review some important regions of the cortex. You should recall the location of the prefrontal lobes, particularly, in front of the motor and premotor cortex. All of the neocortex is important for memory, but the prefrontal lobes may be especially important.

elephant) are retrieved more frequently than unstudied ones. Because conceptual priming depends on meaning, a change in the physical form of stimuli has little influence on conceptual priming.

Conceptual priming is impaired in people with damage to regions of the cortex mediating semantics. Thus patients with semantic dementia whose degeneration affects lateral and anterior temporal lobes show an inability to recognize repeated objects that share a common meaning—for example, two different-looking telephones. But they have no difficulty recognizing the object if it is repeated in identical form (Graham et al., 2000).

Likewise, patients with Alzheimer's disease show preserved perceptual priming but impaired conceptual priming. Functional neuroimaging studies of conceptual priming implicate semantic processing regions, such as prefrontal and lateral temporal areas. As in tests of perceptual priming, tests of conceptual priming lead to decreases in activation in those regions (Buckner et al., 1998; Schacter et al., 2004). Asking people repeatedly to generate examples of "animals" results in *reduced* activation in the same regions.

Numerous studies have shown that priming on a variety of tests is normal in amnesic patients. This applies to most tests of perceptual and conceptual priming, indicating that the MTL does not contribute to them.

4.3 Amnesia can impair working memory

We have already encountered examples of patients, like Clive Wearing and HM, who seem to have spared short-term memory but impaired long-term memory. Tim Shallice and Elizabeth Warrington (1970) reported one of the earliest recognized cases of a patient, KF, with the opposite pattern of impairment: a severely impaired short-term memory but apparently intact long-term memory. For example, when asked to recall short lists of spoken digits, the *digit-span task*, KF could recall only one or two items reliably (as compared to a typical digit-span of around seven items). Still, KF had comparatively normal speech-production abilities and could learn and transfer new information into long-term memory. The finding that a patient with severely impaired short-term memory could still transfer information into long-term memory presented a challenge to the standard hypothesis posited that a unitary short-term memory serves as the gateway into long-term memory. Baddeley's working memory model suggested that if verbal rehearsal is impaired, the visuospatial sketchpad might be used to compensate (see [Figure 9.3](#)).

Indeed, the short-term memory impairment in patient KF, and a number of similar patients reported since, seems to be tied to particular types of information. For example, while these patients struggle to remember verbal items when presented auditorily, their performance is considerably improved when the items are presented visually. What might account for this pattern of findings? Baddeley's answer is that visually presented items can be coded directly into the visuospatial sketchpad, thus avoiding the damaged verbal rehearsal loop.

Neuroimaging has helped to clarify different kinds of memory. These include the distinction between verbal and visuospatial maintenance subsystems (e.g., Smith et al., 1996), the dissociability of storage and rehearsal in verbal maintenance (Awh et al., 1996; Paulesu et al., 1993), and the assumption of a central executive processor that mediates the

behavior of the subsidiary maintenance subsystems (e.g., Curtis & D'Esposito, 2003). In general, neuroimaging studies have tended to support the basic model (Hartley & Speer, 2000; Henson, 2001; Smith & Jonides, 1998).

4.4 Habits and implicit memory tend to survive amnesia

One of the earliest demonstrations of preserved memory in amnesia was on tests of learning perceptual motor skills called *procedural memory*. Corkin (1965) and Milner (Milner, Corkin, & Teuber, 1968) showed that HM was able to learn and retain a pursuit-rotor task, keeping a pointer on a moving target. HM showed improvement on these tasks even months later, though he could not recall doing it even minutes afterward if he was distracted. These findings have been repeated in other cases.

Procedural memory depends on regions like the basal ganglia, which interact with the neocortex. Patients with impaired basal ganglia due to Parkinson's or Huntington's disease show little or no improvement after practicing sensorimotor tasks (Gabrieli et al., 1994; Kaszniak, 1990).

Functional neuroimaging studies also show that learning on the implicit serial reaction-time (SRT) task¹ is associated with activity in the basal ganglia but not with MTL activity.

Suppose you are asked to read a set of words and then your memory for them is tested a week later. We could test your memory directly by asking you to recall as many of the studied words as you can remember or to recognize the words by picking them out from a list of old and new words. If the interval is long enough, you are likely to recall or recognize only a small subset of the items and mistakenly classify old words that you studied as new ones that did not appear on the list.

However, if your memory is tested indirectly by asking you to read the words as quickly as you can, you will be able to say old words faster than new words. The old words are *primed*. On such an indirect test no mention is made of memory, and the subject is typically not even aware that memory is being tested. Yet by looking at how quickly subjects read a word, we can tell whether the previous experience left a residue in memory. The same result can be seen in amnesic patients who cannot recall studying the words at all.

In the case of conceptual or semantic priming, words such as *food* may increase the processing efficiency of words like *water*, even though they share little perceptual content. Priming can be viewed as a way of tapping into the general tendency of the brain to engage in predictive processing at every moment.

Perceptual priming is based on alterations of perceptual representation in posterior neocortex associated with perceptual processing. Conceptual priming is associated with alterations of conceptual systems in prefrontal cortex.

In summary, amnesia due to bilateral damage to the MTL seems to be primarily a disorder of *episodic memory*, resulting from impaired transfer of information from working memory into long-term memory. Because memories acquired long before the onset of amnesia are relatively spared, it is believed that the hippocampus and related structures in the medial temporal lobe are needed only temporarily to hold information in memory until they are consolidated elsewhere in the brain, presumably in neocortex.

¹ The serial reaction-time task has been widely used to study cognition. It uses a series of presentations of a stimulus along with a response—for example 1-2-3-4. This task is used to assess aspects of learning and memory such as the role of context in learning.

5.0 A DEBATE: IS CONSCIOUSNESS NEEDED FOR EPISODIC LEARNING?

We learn about objects and scenes by paying attention to them. As mentioned in [Chapter 8](#), the most obvious result of selective attention is that we tend to become conscious of the objects of attention, as we can prove by reporting our conscious experiences. Episodic memory is generally defined as memory for specific conscious episodes, like the sight of a coffee cup. However, we have also cited evidence that the hippocampal system can be stimulated by unconscious events, such as a subliminal picture of snakes or of emotional facial expressions.

Whether stimuli need to be conscious to lead to episodic memory is therefore a subject of debate. Because it is difficult to ensure that conscious and unconscious brain stimulation lead to comparable MTL activity, the results of that debate are still unclear.

5.1 Attention and learning

A great deal of learning happens simply when we pay attention to something new, and especially if we interact with it. If you learn to play a video game, you might not try to memorize anything deliberately, but simply by playing the game you learn more and more every time you try it. You never need to have a conscious goal of memorizing them. They are simply acquired by conscious exposure. This is labeled “incidental learning,” because the process of learning occurs as a spin-off from merely paying attention. It seems likely that in natural situations much of our learning occurs incidentally.

Learning works best when you pay attention without being distracted. Trying to study in a place where lots of interesting things are happening tends to interfere with learning. Psychologists have used “divided attention” or “dual task” techniques to understand the role of attention (and consciousness) to memory. In a typical study, participants are asked to learn material, like words or pictures, while at the same time having their attention diverted by another task, like tracking a dot on a screen or rehearsing letters in short-term memory. Learning under divided attention is much worse than learning with full attention. Successful encoding requires attention and presumably consciousness.

Exactly why is not well understood. One possibility is that deeper processing requires time, and divided attention may limit the time for encoding. Another possibility is that consciousness is a necessary contributor to memory. If one is not fully conscious of the processed material, learning will suffer accordingly. A third possibility is that attention limits elaboration or organization, both of which are known to improve learning and memory.

A PET study by Fletcher and colleagues (1995) found that activation of the left inferior prefrontal region is reduced under divided attention. This finding was repeated by Anderson and colleagues (2000), with the additional finding that divided attention also reduced activity in the left medial temporal lobes, regions known to be important for verbal memory.

Memory and learning have both conscious and unconscious aspects. If we think about three phases—learning, retention, and retrieval—we can lay out the possibilities in a $3 \times 3 \times 4$ matrix. Of the three, retention is generally viewed as unconscious, although it is shaped by conscious experiences. Learning is often thought to require consciousness, and, intuitively,

we certainly try to learn things by paying attention and therefore becoming conscious of what we want to learn. That is perhaps the most basic learning strategy we have as human beings.

However, there is some evidence for learning without consciousness, especially in the case of biologically or emotionally important stimuli. Learning unconscious input is often confused with “implicit learning,” but these are very different types of learning. When a young child learns its first language, the parents often repeat a word many times, using the singsong that we all tend to use with small children. Toddlers are very attuned to words, and they repeat them spontaneously. It is clear enough that they are conscious of the words and phrases they hear. While it takes time for young children to learn the difference between the sounds of /ba/ and /pa/, these phonemic distinctions in their native language are generally learned in the first two years of life. Thus children who know their native phonology are conscious of the speech sounds that are shared by most native speakers.

However, children are not known to consciously learn the rules of syntax—whether a word is a noun or a verb, for example, or whether the verb of a sentence comes before the object. Many perfectly fluent speakers never learn the rules of grammar at all. It therefore seems that syntax is learned implicitly. That idea has been verified many times by asking people to learn “miniature grammars.” These are typically learned without consciously knowing the sequencing rules of words or other symbols.

“Implicit learning” therefore involves conscious elements, like words, from which a child seems to infer a set of syntactic rules and regularities that are not conscious. Many other examples of unconscious inferences are known in perception, problem solving, and language. It seems that implicit learning has a conscious component, therefore, but that it also has an unconscious rule-inferring component.

However, implicit learning tasks always ask subjects to pay attention and become conscious of a set of stimuli. It is the rules and regularities underlying those stimulus sequences that may be learned without consciousness, just as we normally learn the rules of natural language without knowing those rules explicitly. But we must hear spoken words and phrases consciously for implicit learning to occur.

The terms *implicit* and *explicit memory* are used in the context of remembering—that is, retrieval of stored information. Explicit memory refers to memory with conscious awareness—namely, memory of which the individual is aware, can declare its existence, and comment on its content, either verbally or nonverbally (Schacter, 1987). For this reason, such memories also are known as *declarative memories* (Cohen & Squire, 1980; Ryle, 1949). They are the kind of memory to which we typically refer in everyday conversation when we ask, “Did you remember to call your aunt to thank her for the birthday present?” or “Do you remember who won the Academy Award for best actor or actress?”

5.2 Implicit and explicit aspects of learning

Implicit learning is not accompanied by conscious awareness of a memory; the existence of a memory is inferred indirectly from the effects it has on behavior. Priming effects are used extensively to test for implicit memory. “Priming” refers to the effect of a stimulus in creating readiness for a similar one. For example, showing a picture of a face will increase the

processing efficiency of a following face, as measured by faster reaction time and greater accuracy. Priming can be either perceptual or conceptual.

5.3 Implicit learning in language

The past few years have witnessed the emergence of increasing studies of implicit learning in language. This is perhaps not so surprising in that language acquisition, like implicit learning, involves incidental learning conditions. Further, cogent use of language likewise does not require explicit knowledge of grammar. Recently, several authors have begun to explore this connection empirically. For instance, Saffran and colleagues (1997) showed how incidental exposure to artificial language-like auditory material (e.g., *bupadapatubitutibu...*) was sufficient to enable both children and adult subjects to segment the continuous sequence of sounds they had heard into the artificial words (e.g., *bupada*, *patubi*, etc.) that it contained, as evidenced by their above-chance performance in a subsequent recognition test.

Based on these data, Saffran and colleagues suggested that the word segmentation abilities demonstrated by these subjects were due to the transitional probabilities of successive syllables which are higher *within* words than *between* words. Saffran and colleagues interpreted their findings as representing a form of implicit learning. The connection is obvious when one recognizes that language acquisition, like implicit learning (Berry & Dienes, 1993; Cleeremans, 1993) is likely to involve, at least in part, incidental learning of complex information organized at differing levels.

Part of the convergence between language acquisition and implicit learning suggested by Saffran and colleagues can be attributed to the impact of computational modeling on the field of memory research. For instance, connectionist models such as the Simple Recurrent Network have been extensively used with significant success in both the language acquisition and implicit learning domains (Christiansen et al., 1998; Redington & Chater, 1997). In effect, the problems faced in both domains are quite similar: how to best extract structure from a complex stimulus environment characterized by “deep” systematic regularities when learning is incidental rather than intentional. The answer, in both domains, appears to be embodied by distributional approaches.

Figure 9.14 brings out several features of learning and memory. Notice that conscious cognition leads to *explicit* learning and memory retrieval in this figure. An obvious example is deliberately trying to memorize a technical term in cognitive neuroscience. What may not be so obvious, however, is that *implicit* learning also happens along with learning of conscious or explicit stimuli.

Thus Figure 9.14 shows both explicit or conscious *and* implicit or unconscious learning. Episodic memory is the storage of conscious episodes (also called autobiographical memory). Semantic memory, usually viewed as memory for facts, is also conscious, in the strict sense that people can accurately report the facts they believe. This is the standard operational definition of conscious brain events (see Chapter 8). Finally, perceptual memory capacities, such as our ability to “learn to hear” music and art, also involve conscious, explicit kinds of memories.

On the right-hand side of Figure 9.14, we also see the learning of implicit memories. Infants may hear sequences of speech sounds, but they are not explicitly learning the rules and

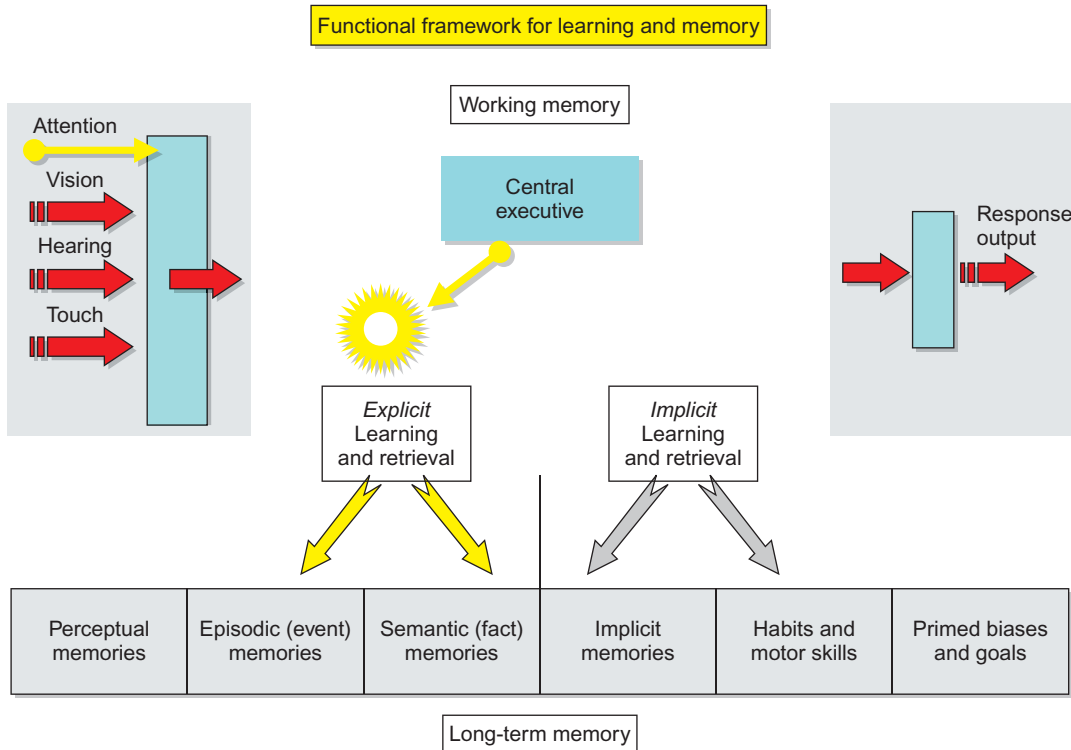


FIGURE 9.14 Implicit and explicit (conscious) learning. This version of our functional diagram suggests that there are two ways for information in working memory to lead to long-term memories. In the case of “explicit learning,” a conscious event (an “episode”) is registered in episodic memory (gray boxes at the bottom). However, a great many things we learn are implicit, such as the implicit inferences we make from the two sentences like “The glass broke. It shattered on the kitchen floor.” The complete meaning of those sentences is stored in memory, including the idea that glass is brittle. This is an example of an implicit memory. Source: *Baars*.

regularities of grammar. Those are apparently learned unconsciously, as we will see later. In general, implicit learning is often evoked by explicit, conscious events, but it often goes far beyond the events given in conscious experience (Banaji & Greenwald, 1995). Overpracticed habits and motor skills are also largely implicit. As we will see, priming effects are often implicit. Contextual phenomena are often implicit, such as the assumptions we make about visual space, the direction of the incoming light in a visual scene, the conceptual assumptions of a conversation, and so on. These are often hard to articulate, implicit, and to some degree are unconscious (Baars, 1988).

Figure 9.8 shows one version of learning with consolidation, in which input into the neo-cortex and the hippocampal regions (MTL) evoke an active state, with neuronal processes making new synaptic connections. As just mentioned, immediate memory is encoded in improved synaptic connectivity between billions of neurons in the neocortex. Normal sleep, especially the slow wave stage, is important to turn these temporary connectivities into long-lasting memory traces.

6.0 DOES SEMANTIC MEMORY COME FROM EPISODIC TRACES?

6.1 Semantic memory is different

There is good evidence that semantic memories may be formed from repeated, similar episodes. Attending a high school is a long series of episodes. We may be able to recall dozens of those episodes, but much of the time they seem “smeared” together in memory in the semantic belief that “I attended such-and-such high school.”

Figure 9.15 shows how episodic and semantic memories may be related in the brain. Specific episodic memories are shown in the pictures of a man cooking on a barbecue grill, presenting flowers to a young lady, painting a picture, and playing golf. These are separate autobiographical memories, remembered as conscious events. Above these pictures, a small semantic network combines all these very specific and richly detailed episodes into a single figure: a semantic network of a man who cooks, loves, paints, and plays golf. The semantic network is more abstract and general than the episodes about particular events in the life of the person. Moscovitch (2006) claims that the bottom row of episodes depends on the MTL, and the top figure depends on neocortical modules.

Episodic memories typically:

1. have reference to oneself
2. are about a specific time
3. are *remembered* consciously, as if we reexperience them
4. can be forgotten
5. are *context-sensitive*, with remembered aspects of time, space, people, and circumstances

In contrast, semantic memories (Figure 9.16) generally:

1. have reference to shared knowledge with others
2. are not organized around a specific time period
3. give a “*feeling of knowing*” rather than a fully conscious recollection of the original event
4. are less susceptible to forgetting than specific episodes
5. are relatively independent of context

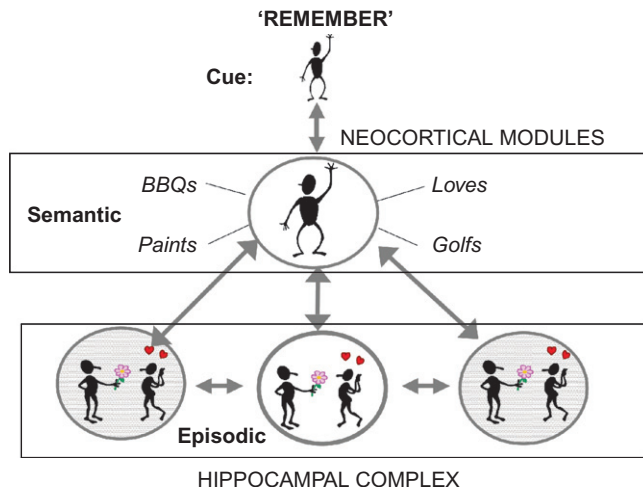


FIGURE 9.15 From episodic to semantic memories. Semantic memories are assessed by feelings of knowing, which can be very accurate. However, they do not require active reconstruction of the original episode and can apparently be neocortex without the aid of the hippocampal complex. Source: Moscovitch.

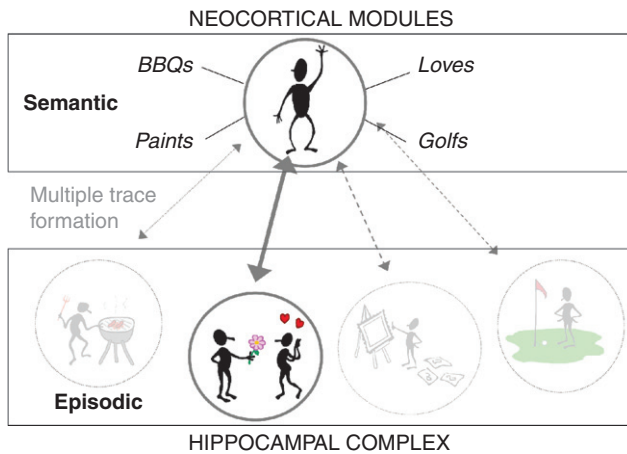


FIGURE 9.16 How semantic and episodic memories may be related: semantic memories may be the neocortical residue of many episodic memories. Thus one may have many experiences with the stick figure, such as watching him or her cooking a barbecue, presenting flowers to a young lady, painting, and playing golf. Over time, these episodes may be forgotten, and only the semantic knowledge remains that this is the kind of person who does all those things. These are multiple traces that are created each time there is another episodic experience with this person. Semantic memory may require only the neocortex (particularly the temporal and frontal lobes). Episodic information may require both the neocortex and the hippocampal complex. Source: *Moscovitch, 2004, modified with permission.*

Tulving (1985) introduced the remember/know procedure, asking participants to report their conscious experience when they recognize studied items. If they believe an item was studied before, they must decide whether they *remember* the item (i.e., they can reexperience episodic details about the event) or whether they *know* the item (it feels familiar). Local hippocampus seems to affect only “remember” judgments. Memory based on feelings of knowing is spared after hippocampal damage (Moscovitch & McAndrews, 2002; Yonelinas, 2002). Similarly, in functional neuroimaging studies, hippocampal activation is associated more with remembering than familiarity (Eldridge et al., 2002; Yonelinas et al., 2005).

When you are asked if the face of a particular person is familiar to you, like the movie star Brad Pitt, on what basis are you making your judgment? Are you relying on your semantic memory, episodic memory, or both? Westmacott and colleagues (2004) have shown that *both* systems may contribute because performance on semantic tests is better if the participant also has some episodic memory associated with the famous name.

Semantic dementia is diagnosed in a subset of Alzheimer’s disease patients who show widespread deficits in understanding meaning, often with spared perceptual abilities. These patients, whose degeneration of anterior and lateral temporal lobes leads to semantic loss, can identify common objects only if they can make a personal association to them. For example, they can identify a vase only if it is one that belongs to them (Graham et al., 1999; Snowden et al., 1996).

Remarkably, however, if the MTL is injured very early in development, during infancy, semantic memory develops relatively normally in most cases (Vargha-Khadem & Mishkin, 1997). However, episodic memory still remains impaired without an MTL. What these findings suggest is that early in life, the semantic system has the capacity to acquire knowledge on its own, without the help of the episodic system (MTL).

Metacognition is an important aspect of normal memory retrieval. A memory trace may be retrieved spontaneously, or more often by cues or reminders. A cue could be as simple as

“Recall the words you just studied” or as complex as “Describe in detail what you did today.” The kind of self-monitoring we tend to do when we try to remember a missing word is a kind of metacognition that involves the prefrontal cortex.

7.0 CONTROL OF MEMORY

How we interpret and deal with material in our memory is determined by our current goals and concerns, as well as by our existing knowledge. Sensory and internal information may be brought to consciousness using attention. Once it becomes conscious, a number of theorists maintain that information is rapidly *encoded* into long-term memory (e.g., Moscovitch, 1992). There is also evidence for some unconscious learning, but so far only unconscious fear conditioning has been shown to result in long-term memory (LeDoux, 1996). In general, conscious exposure correlates well with learning.

7.1 Working with memory: the frontal lobe works purposefully *with* memory

We have a measure of control over what we encode and what we retrieve from memory. How can we reconcile this with other facts we know about how memory works? One solution is that the frontal lobes control the information delivered to the medial temporal system, initiate and guide retrieval, and monitor and help interpret information that is retrieved. The frontal lobes act as *working-with-memory* structures that control the more automatic medial temporal system and give a measure of intelligence and direction to it. Such a complementary system is needed if memory is to serve functions other than mere retention and retrieval of past experiences (Moscovitch, 1992).

7.2 Prefrontal cortex in explicit (conscious) and implicit (unconscious) learning and memory

Working memory may help us to learn both explicit (conscious) and implicit (unconscious) information. One of the functions often attributed to consciousness is the integration of information across domains. In a very illuminating study, McIntosh and colleagues (1998) had subjects perform in a trace conditioning task, which requires the person to make an association between a color and a tone separated by a blank delay of about a second. Using PET, McIntosh showed that learning, and the conscious awareness that accompanied it, was associated both with frontal activation and with coherence of activation across many areas of the cortex. McIntosh and colleagues speculated that consciousness is associated with activation in the prefrontal cortex, which, in turn, leads to a correlated pattern of activity across disparate regions of the cortex.

It remains to be seen, however, whether frontal activation preceded or followed conscious awareness of the association. If the prefrontal cortex plays a pivotal role in consciousness, as many people have speculated, deficits on all memory tests dependent on consciousness should be observed in patients with frontal lesions. However, so far, the evidence

indicates that the effects of frontal lesions are much more selective and not nearly as debilitating as lesions to the MTL and related nuclei of the thalamus.

The prefrontal cortex (PFC) contributes to implicit learning and memory if it requires search, sequencing, organization, and deliberate monitoring. Implicit learning of language is a good example. Even though we rarely try to make the rules of grammar conscious and explicit, we nevertheless need to direct our attention to the order of words in a sentence to learn a language implicitly. It is likely that unconscious inferences help us to discover rules or regularities, provided that we pay “conscious attention” to a series of words, for example, from which we can discover the implicit.

7.3 Prefrontal—storage or executive control?

The prefrontal cortex is an important site for working memory function. According to one interpretation, this brain region participates directly in the storage of information. However, the PFC is also associated with control of working memory. Patients with left temporo-parietal damage may have a storage deficit in working memory and can’t perform even simple maintenance tasks with auditory-verbal information. The findings from these patients can be contrasted with those from patients with damage to the PFC (D’Esposito & Postle, 1999). Some PFC patients show little impairment in passive maintenance of information over a delay. However, these patients were impaired in mentally *manipulating* or *acting upon* briefly stored information. Perhaps PFC supports the mental “work” performed on stored information, rather than as a site for storage itself. (D’Esposito & Chen, 2006).

One possibility is that different parts of the PFC do different things. This is the so-called “maintenance” versus “manipulation” distinction. It has been argued that *all* of the PFC has an executive function in working memory but that different subdivisions do this at different levels of analysis (Ranganath, 2006). The PFC may enhance relevant information in other parts of the cortex. When the information is specific, more ventral PFC regions are engaged. When the information involves integration of multiple items in memory, the dorsal PFC regions are engaged. More frontal regions of the PFC may coordinate and monitor different PFC regions. If this is true, the main role of the PFC is not working memory but *working with memory* (Moscovitch, 1992; Moscovitch & Winocur, 1992).

7.4 Real memories are dynamic

Traditionally, a memory is considered to be a stable record of an event, which can be recalled in the same form it was learned. In this commonsense view, memories can be retrieved, examined, and played back like a high-fidelity recording. Memories can also be forgotten without affecting other cognitive systems.

There are reasons to question this idea. One is that real memories are rarely accurate. The *process view* considers memory to be a product of a dynamic process, a reconstruction of the past influenced by past and current conditions, anticipations of future outcomes, and other cognitive processes. In the process view, memory is based on stored information but is not

equivalent to it. It is dynamic and mutable and interacts with other processes. Thus two people experiencing the same event may have different memories of it. It is not simply that one person is right and the other wrong, but each person's outlook, knowledge, motivation, and retentive abilities may alter what is retrieved.

Everyone's memory changes with time. We forget most of what has happened within minutes or hours, and what remains is commonly reorganized and distorted by other knowledge or biases. We would not want computer files or books to be that way. We do not want files to decay over time or to leak into neighboring files. Computers and libraries are designed to keep everything as distinct and stable as possible. Yet normal memories do fade and are often confused with others.

Try to reconstruct in as much detail as possible all the things you did two weekends ago, in the exact order in which you did them. To do that, most of us have to search for cues to determine exactly what we did. Having found a cue, there is a process of reconstruction, especially in trying to figure out the sequence of events. Did I meet my friend before I spoke to my parents or afterward? Did I go shopping, and what was the order of the stores I visited? In each store, in what order did I look at the merchandise and buy it? You can try this with a recent movie and then see how accurate your memory is by checking it against a copy of the movie.

To answer these questions, you must draw on a body of knowledge and inference that is unlike anything that is needed when you enter a file name to access a computer file or use a call number to find a library book. You may confuse what you did two weekends ago with what happened another time. As we will see, some patients with brain damage have a disorder called *confabulation*, in which they make up false memories without any intention of lying and without any awareness that their memories are incorrect.

8.0 SUMMARY

The medial temporal lobes (MTL) are crucial to episodic memory. Amnesia patients with bilateral damage to the MTL are unable to remember specific past episodes or to learn new ones. However, implicit memory may be spared in these patients. Patients suffering from semantic deficits typically have damage in the temporal lobe and the prefrontal cortex. Such patients with semantic dementia, for example, may retain episodic memories but are impaired on semantic tasks.

While explicit memory is assessed by accurate memory reports, implicit methods like priming and sensorimotor performance are used to assess implicit memory. Much of our learning is implicit, such as the learning of language. However, implicit learning requires conscious and attentive orienting to the stimuli to be learned. What is unconscious about implicit learning is not the original stimuli but the inferential regularities that allow us to organize those stimuli. Sensorimotor skills are guided by the frontal cortex in collaboration with the basal ganglia and cerebellum. After overpracticing predictable tasks, such learned skills become less conscious and seem to rely only on subcortical structures like the basal ganglia.

Human memory involves multiple brain regions: the MTL for explicit episodic learning; the prefrontal cortex for metacognition, maintenance, and use of memory; and sensory regions for perceptual and sensory memories. The cerebellum and basal ganglia are required for sensorimotor skill learning, in interaction with the frontal lobes. The sensory and motor halves of the cortex are in constant dialogue with each other, as when we hear ourselves speak. Finally, the amygdala is involved in emotional learning.

9.0 DRAWING EXERCISES

1. Fill in the missing labels in the functional diagram given in [Figure 9.17](#). Define each of the terms.
2. Label the brain regions that are relevant to learning and memory in [Figure 9.18](#).
3. Label and describe some memory regions in [Figure 9.19](#).

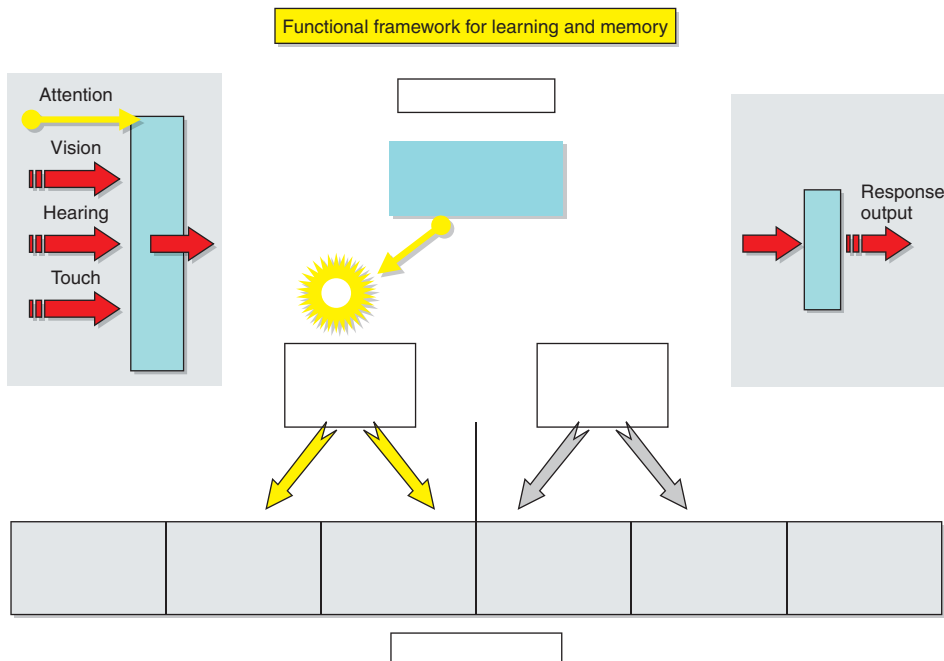


FIGURE 9.17 Fill in the missing labels in this functional diagram. Define each of the terms.

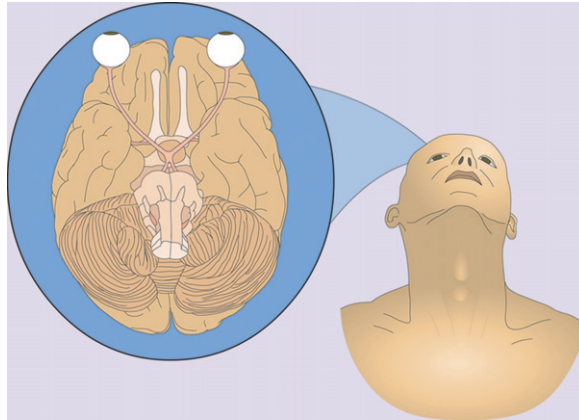


FIGURE 9.18 Label the brain regions that are relevant to learning and memory.

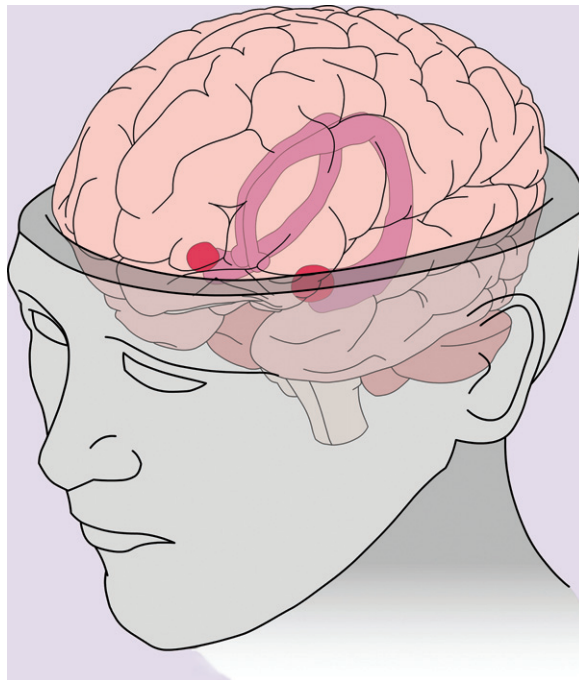


FIGURE 9.19 Label and describe some memory regions in this figure.

Thinking

O U T L I N E

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MICRONESIAN NAVIGATION



Sea travel may have started 40,000 to 100,000 years ago. Micronesian peoples developed high-level navigational methods over centuries. Long-distance ocean travel requires complex problem solving, immense persistence, travel planning, a star compass, time and distance estimation, hunting and fishing, woodworking and rope making, a specialized vocabulary, coping with adverse weather, special social customs, trading skills, and self-defense. Sailboats and outrigger canoes are historic inventions.

1.0 INTRODUCTION

Cognition involves problem solving. Understanding the sentence you are reading now involves many neural events that interpret retinal light patterns on the back surface of each eye through many layers of analysis (see [Chapter 6](#)). In a real sense, each word and letter is a *problem* for your reading brain to solve. In gaining expertise you have practiced each component for thousands of hours. The result is a fast process that is mostly unconscious but which ends with a conscious appreciation of *these words* that you are reading now, perhaps *echoed in your inner speech*, and most important, with a *conscious interpretation* of what it all means.

In that broad sense, this whole book is about the ways the brain solves problems. Problem solving implies an initial state (A) and a goal state (B), with some set of goal-driven procedures to get from A to B. [Box 10.1](#) presents a “Tower” puzzle that is used in problem-solving experiments. Formally, problem solving can be described in terms of a *problem space*, a kind of a maze, showing end goals, subgoals, and step-by-step progress through the maze. Mathematics, computer science, and psychology have added to our understanding of problem solving, but its brain basis is only beginning to be understood.

[Figure 10.2](#) shows a *problem space* for this version of the Tower puzzle. In this case all possible moves can be shown, as well as all the step-by-step pathways through the maze.

BOX 10.1

A PROBLEM SPACE FOR PUZZLES

Figure 10.1 shows a “Towers” puzzle that is used to test neurological patients. It is helpful to try a few moves for yourself. Towers puzzles can be adjusted in difficulty level. They are designed to be solved only by step-by-step planning, a frontal lobe function.

In serial problems the time from start to finish is a linear function of the number of steps. Over multiple trials, we do speed up. “Time to a correct solution” is therefore a reasonable measure of efficiency.

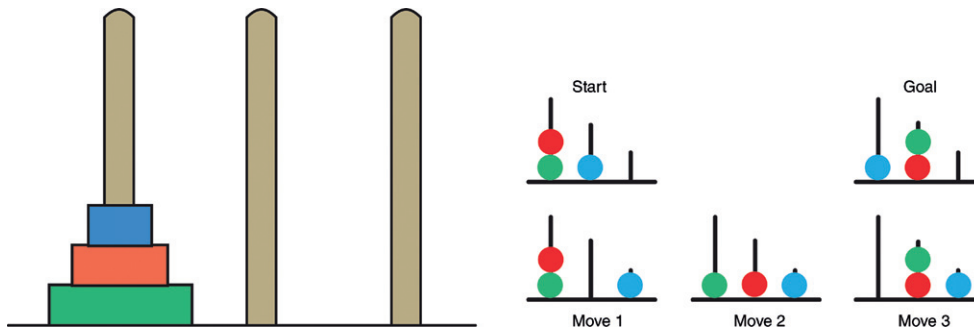


FIGURE 10.1 Shallice (1982) used Tower puzzles to diagnose frontal impairments. The task is to move the rings one at a time, starting with the top ring, until you reach the correct set of rings on the correct peg. The difficulty level of these puzzles can be adjusted. Tower problems have been standardized for testing and have led to a great deal of research. Instructions on effective strategies improve performance for people with healthy frontal lobes. Source: Miller & Wallis, in Squire et al., 2008.

Problem spaces are *formal descriptions*. They tell us about the structure of a problem—not about the human brain—It is important not to confuse the formal structure of a problem space, like chess, with what human beings are actually doing when they play chess. However, as long as subjects have no previous practice, we can predict how long they will take to reach a goal, their errors and self-corrections, and even specific brain activity.

Tower puzzles are useful for diagnosing frontal lobe impairments (see Box 10.1). Problem-solving performance is impaired by brain damage but also by everyday events like drowsiness, fatigue, distractions, alcohol, and anesthetics. On the positive side, drinking coffee or taking the alertness drug Provigil (modafinil) can improve frontal lobe functioning.

In many cases, what looks like a serial problem to newcomers may allow for fast shortcuts for experts, who can use their prior knowledge. Similarly, when we gain expertise in speech, reading, writing, and many other skills, we can process difficult tasks quite fast.

Tower puzzles are useful, but we have to be careful about generalizing to real-world problems, which are often quite different. Real-life problems tend to be complex, vague, ambiguous,

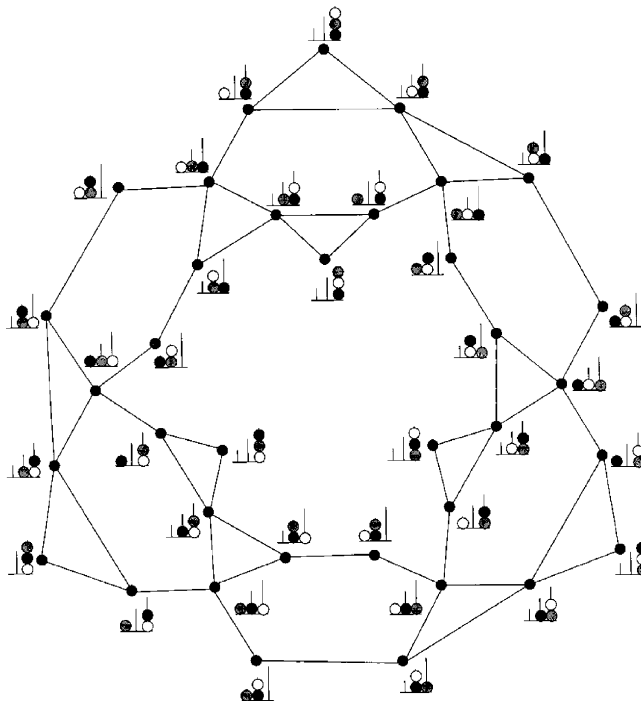


FIGURE 10.2 The problem space for the Towers puzzle shows many possible positions, choice-points, and pathways. Source: Baars, with permission.

or poorly understood. Whole categories of scientific problems are not formally *tractable*—that is, they cannot be solved by conventional mathematical methods.

Further, human beings pick up all kinds of *heuristics*—tricks and tips that help us get to a “good enough” solution faster than Figure 10.2 suggests. Human experts know many heuristics to solve practical problems. For humans to survive as hunter-gatherers during a severe drought, a formal “best solution” to the danger of starvation does not even exist. In Herbert A. Simon’s¹ terms, humans do not “optimize” in those circumstances—that is, look for the very best solution—but “satisfice.” In other words, all we want is a good enough solution, one that will get us through the dry season with minimal losses. The formal problem space of Figure 10.2 therefore might not tell us how people reach their goals in the real world.

The real world often gives us *advantages* we don’t find in artificial puzzle problems, such as the benefits of *prior knowledge*. If we know all the houses on a street, we don’t have to check each one on the way to a friend’s home. A newcomer to the neighborhood may have to think serially by checking each street address, one by one, but with the right knowledge we can go straight to the goal. Navigational problems can often be solved by prior knowledge. If you are familiar with your destination, you may not even bother to pay attention to most of the route going there. You may be allocating most of your attention to other things.

The best way to allocate your limited time and capacity is itself a problem to solve each day. If you are a college student, you may want to allocate your ability to tackle difficult

¹ Dr. Herbert A. Simon was a Nobel Prize laureate (1978 in Economics) and the “Father of Artificial Intelligence”. He died in 2001.

learning to the early morning, when you are feeling fresh and your frontal lobe is working well with the help of coffee. Later in the day you may want to allocate your limited capacity to socializing or just wandering around the campus. Allocation of limited resources is a standard question in economics, and attention (and learning capacity) is a limited resource in life.

Again, there may be no best solution for allocating your time and attention. Late adolescence has many goals, including forming friendships, thinking about life, anticipating employment, and discovering one's lasting values. Academic study is only one of the goals we pursue in college. If you keep in mind your own experiences in reading this book, you will see many examples of problem solving. The act of learning is itself a problem-solving challenge.

1.1 Conscious and unconscious processes

Human thinking comes in two varieties, *explicit* and *implicit*, roughly the same as “conscious” and “unconscious.” In experimental practice they correspond to “reportable brain events” versus “unreportable” ones. Explicit and implicit problem solving is different in several ways, as we know from many careful experiments (Schneider, 2010). Everyday problem solving is a mixture of the two.

Studying explicit thinking seems fairly straightforward, because people can tell us their step-by-step thoughts in a game of chess, for example. By definition people cannot tell us about their *implicit* brain activities, but the evidence for unconscious cognition has now become very strong, and better methods are available to study it (Stacy & Wiers, 2006).

One very important finding from brain imaging is that learning a task can actually *decrease* metabolic brain activity as measured by *functional* brain imaging (fMRI, MEG, EEG, and the like). Functional brain imaging involves indirect measures of large-scale neural firing, which quickly requires new supplies of glucose and oxygen. We can measure the oxygen rise using fMRI (BOLD), and the neural population activity by MEG and EEG.

Figure 10.3 shows an example of the effects of practice in an auditory search task. As you can see in Figure 10.3b, “Controlled processing”, there is a great deal of dynamic brain activity to start with, in order for the subject to score well in auditory search. One auditory search task is to detect a high-pitched piccolo trill against a lower musical background. Auditory search can also involve detecting a specific location of a known sound.

In Figure 10.3c, “Automatic processing”, the subjects are doing exactly the same task after practice, and chances are they are doing it better than before. Practice improves performance. And yet most of the brain activity has disappeared after practice. It seems like a paradox.

What could be happening? It's not that the brain has gotten tired of doing the same thing over and over. Rather, what's happened is *learning*, and as we know from Chapter 9, learning involves changing synaptic strengths when two linked neurons fire together. As a result of active learning, after extended practice the brain is able to do just as well with much less energy expenditure, using strengthened synaptic connections.

When highly practiced, automatic routines become unconscious and therefore difficult to report, but they don't disappear from the brain. Rather, automatic skills are encoded by stronger synaptic connections. It is only the dynamic cortical activity (metabolically expensive) that drops.

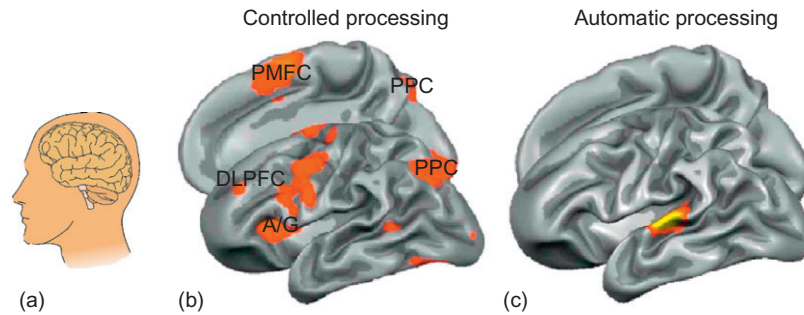
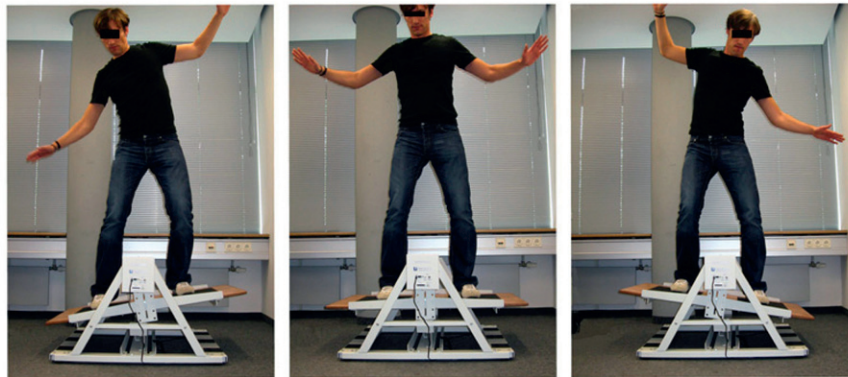


FIGURE 10.3 Cortical activity drops after extended practice. The difference between explicit and implicit problem solving is very clear in these two fMRI scans (b) and (c). Both scans show auditory search for a sound, like locating a piccolo in a marching band. When the task is new and effortful, (b) “Controlled processing”, the cortex activates many regions needed for voluntary attention and control (Schneider, 2011). But after practice, (c) “Automatic processing”, the same task only shows metabolic peaks in auditory cortex. (a) Shows the orientation of the brain scans in the head. Source: *Schneider, 2010*.



(a) MRI scans (s1...s4)



(b)

FIGURE 10.4 A balance board was used to train subjects to keep their balance. Brain scans were taken every two weeks (s1–s4). Source: *Taubert et al., 2010*.

For example, Taubert and colleagues (2010) asked subjects to learn a “skateboarding” task over several weeks (Figure 10.4). Their job was to stay on a wiggly balance platform as long as possible. Behavioral measures improved steadily.

Keeping your balance involves a kind of problem solving that can improve with practice. Balance includes control of the hands, legs, and torso. When the platform tips to one side, the subject needs to lean to the opposite side with precise timing so the countermovement is not

too much and not too little. Once the limbs swing to counter the unstable board, they have to be equalized to both sides very quickly or the subject will overbalance and fall off.

Because we know which cortical regions are involved in controlling the limbs (see [Chapter 4](#)), we know where to look for cortical changes as the balancing task is learned (Taubert et al., 2010). [Figure 10.5](#) shows important results.

As we know, learning results in greater synaptic strength, which requires the physical growth of neurons, axons, and synaptic terminals. However, the dynamic activity actually decreases with practice, just like [Figure 10.5](#). Once the balancing task is learned, the brain has to do less active work to reach the goal.

Using our traffic metaphor from [Chapter 3](#), the brain works dynamically to solve the problem when it is new, and it may have to send signal traffic along many different pathways, showing up in brain scans as high-energy activity. In a real city, traffic engineers constantly

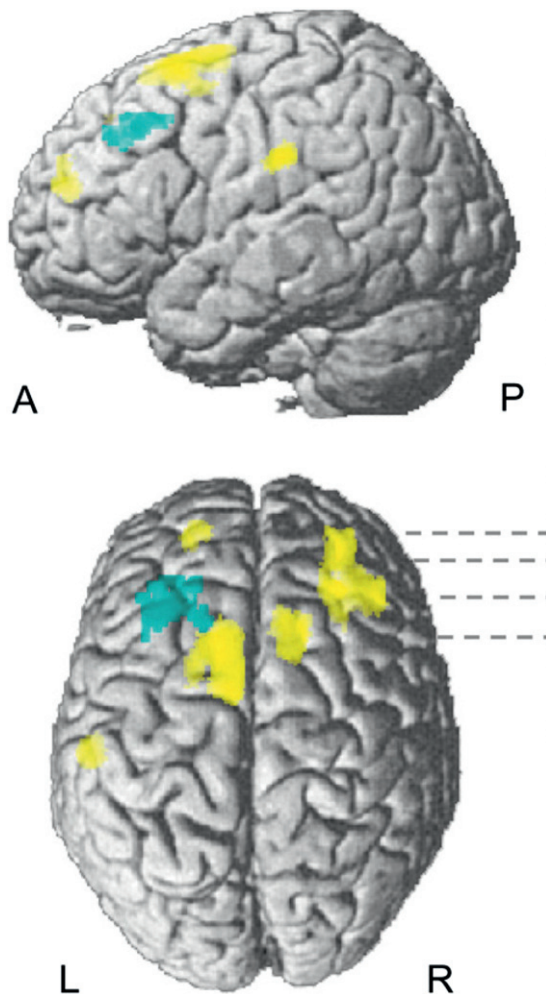


FIGURE 10.5 Learning changes both dynamic and structural features in the cortex. The yellow areas represent *increases* in the density of the motor cortex after two weeks of practicing the balance task. The bluish (cyan) color represents a *decrease* in dynamic cortical activity. The brain has learned to do the task with minimal energy expenditure. Dynamic problem solving seems to be converted into long-lasting structural changes. Sensorimotor learning like this also causes changes in the basal ganglia, cerebellum, and sensorimotor pathways. Abbreviations: A = Anterior, P = Posterior, L = Left, R = Right. Source: Taubert et al., 2010.

monitor traffic flow, making street improvements and adding new routes as traffic increases. The brain essentially builds bigger streets as well when its traffic flow becomes denser in some part of cortex. We could imagine road-building crews following high-density traffic to expand the carrying capacity of the most frequently used roads. In the brain those structural improvements are carried out by strengthening synaptic links, a process that requires protein production.

White matter pathways may continue to grow until age 20 or 30. They reflect a mix of genetically coded and highly practiced routines for solving everyday tasks. Not all tasks fade from consciousness after practice. For example, sensory events seem to stay conscious even after many practice sessions, especially if subjects interact with the sensory input and if they are important. Skilled drivers may have seen traffic signals turn green thousands of times, but we don't lose conscious access to green lights when we drive. In some cases, like listening to music, we may improve our ability to experience it and understand it. Attentional habits can also be highly practiced, improving our ability to bring selected targets to consciousness (see [Chapter 8](#)).

2.0 EXPLICIT THINKING

Mental arithmetic and chess playing use *explicit* thinking. We can walk through such problems consciously and deliberately, step by step. Explicit thinking often has clear, conscious subgoals that must be finished before the main goal can be reached.

Compared to implicit thinking, explicit cognition requires the following:

1. Greater executive control and decision making
2. More conscious involvement
3. More intense judgments of mental effort
4. Much wider metabolic activity in the brain, as measured by fMRI, EEG/MEG, or direct brain recording

However, after years of practice, explicit problem solvers, like chess experts and mental calculators, tend to become more intuitive and less conscious of the details of their thinking. Explicit cognition may become more implicit with practice.

Explicit thinking often uses symbols, like words or visual images. In neuroscience terms, symbols can be defined as conscious events that refer to accessible knowledge and/or a category of events in the world. A phrase like “this coffee cup” is an example of a symbolic string that evokes a meaning representation in the brain and that in turn refers to an event in the world.

Humans are constantly inventing symbols for new domains like computer programming, avatar games, and texting. Some recent examples are vector graphics, Twitter, and C++. By capturing a large body of knowledge with a new word, we make it easier to manipulate concepts within the limits of working memory.

Working memory has a limited number of “chunks,” but each chunk can refer to a very large domain of memory or knowledge. Defining the meaning of a word like *avatar* might take ten ordinary words, but once you understand it, you can put several meaning-packed chunks into a single phrase. The statement “I twittered my avatar in C++” would take a lot longer to say without those special words.

Our vocabulary is a vast collection of ready-made labels and concepts to help us think explicitly. Educated people may have a vocabulary of 100,000 words, a very large archive of accessible knowledge. One rule of thumb of explicit problem solving is to simplify a problem to a few symbols that can be held in working memory. Most fundamental equations in the sciences and mathematics can be simplified, like the famous Einstein mass-energy equation $e = mc^2$. Each symbol in the equation refers to a large network of other symbols and equations, which can often (but not always) be measured in nature.

Most of our problem solving is not logically airtight like an equation, but we all need to simplify a great deal of knowledge to tackle real problems in life. A decision to attend a particular school or college ultimately comes down to a checklist, comparing several schools on the most important criteria. We somehow have to distill a vast amount of information into a set of paired comparisons.

Likewise, your choice between two reading lenses comes down to “A-B comparisons.” That method was developed by sensory scientists two centuries ago, and your optometrist is still using it today because it is well suited to our immediate memory limits. If we had a little number scale attached to our eyes, we could imagine measuring visual acuity in a different way. Human brains and human vision did not evolve that way.

We could use computers, an abacus, memory techniques, or formal symbols to extend the limitations of our working memory. The kings of England are said to have hired a “royal remembrancer” to keep the king’s decisions in mind. Popular writing systems are too recent to have changed our brains very much (2,500 years at most), and language itself is believed to go back only 100,000 to 200,000 years. Unfortunately humans did not have powerful computers until very recently. Explicit thinking was done by intelligent and hard-working people, and that is what we will explore in this chapter.

Existing knowledge works together with conscious events during explicit problem solving. It is possible that implicit thinking uses many of the same functions that have become highly practiced, automatic, and largely unconscious. In a broad sense, working memory is the domain of problem solving, language, and thought (see [Chapter 2](#)). It is “the set of mental processes holding limited information in a temporarily accessible state in service of cognition” (Cowan et al., 2005).

We need working memory to perform mental arithmetic, to carry on a conversation, or to solve a path-finding problems like “How do I walk home from here?” You cannot understand the sentence you are reading now without keeping words, ideas, and syntax in immediate memory. When we think about a problem, we constantly use inner speech and visuospatial thinking, directing attention to what is currently most important. As discussed in [Chapter 8](#), attention leads us to become conscious of sensory events, of inner speech and action planning. Finally, whatever we actively think interacts with what we already know—our long-term store of memories, knowledge, and skills. Every word in this sentence is also part of our long-term vocabulary. Every eye movement you make is based on long-practiced routines (see [Chapter 9](#)). Thus all the components of the functional diagram ([Figure 10.6](#)) come into play in the realm of thinking and problem solving.

Surprisingly, much of this chapter is not about the colored boxes in the functional diagram but about the row of gray boxes along the bottom. The colored boxes refer to active processes, those that require neuronal firing and integration. But they constantly interact long-term memories. Such permanent stores may not show up directly in functional brain imaging because they are encoded in the connective strengths between neurons. Methods like

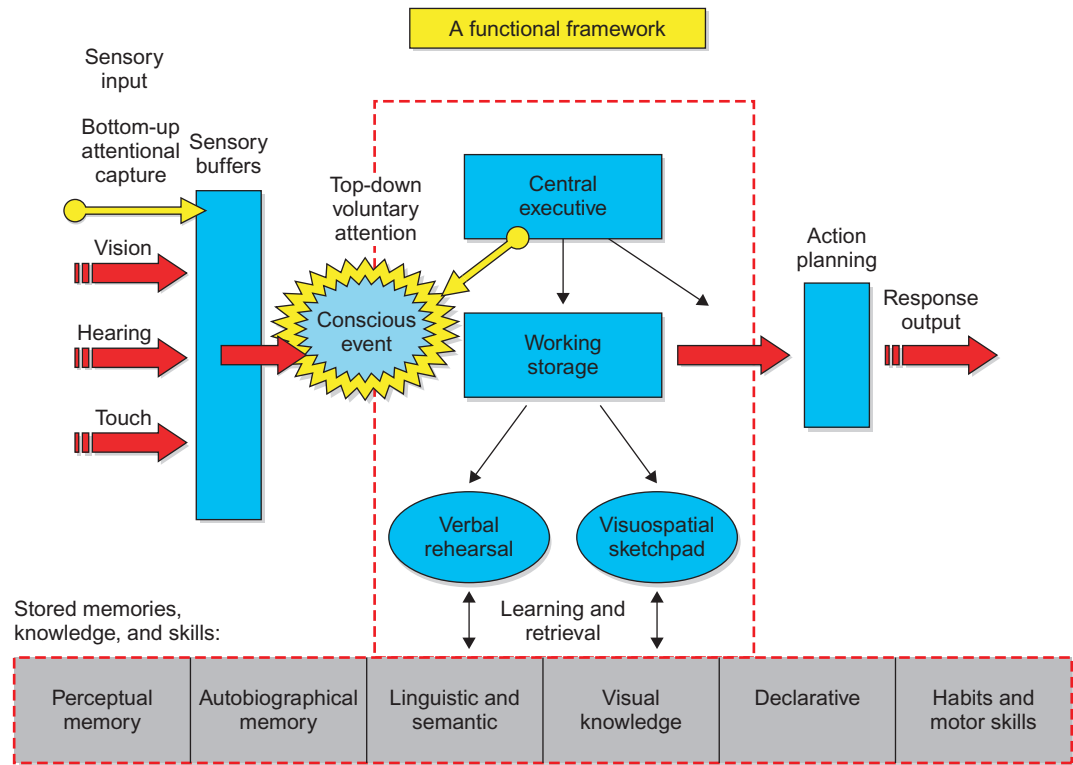


FIGURE 10.6 Explicit problem solving in the functional diagram. The blue boxes outlined by the dashed red line include working memory, attention, and conscious focal events. But all the active boxes and ovals in the upper rectangle makes use of long-term memory traces of all kinds, many times per second. The distinction between the upper and lower rectangle (surrounded by red dashed lines) is therefore important, but there is still constant traffic from the long-term memories to active and explicit processes. Every new problem we try to solve demands focal attention—what we are conscious of. According to Cowan’s (2008) intensive studies, “what appears to be a general capacity limit in working memory ... is closely related to the contents of the conscious mind.” Source: Baars, with permission.

functional magnetic resonance imaging (fMRI) activity may therefore under-represent the vast amount of long-term knowledge.

Oral cultures use spoken patterns, like poetic rhymes, alliteration, melodic chants, or poetic meter. That is how young children often learn their “ABCs” through a song. It’s not a bad way to learn brain anatomy either.

2.1 Working memory includes attention, conscious contents, and learning

Figure 10.6 shows what scientists have called “working memory” as a key to explicit problem solving, but such labels are somewhat arbitrary. The red-outlined boxes in the diagram include selective attention, conscious contents, and executive control. Experimental studies

show that these functions can be separated from one another so they are not just different labels for the same thing. However, in everyday life all these elements work together.

Experiments may be designed to separate working memory and other cognitive functions. For example, in some working memory experiments, activity from single neurons in the prefrontal cortex is recorded in monkeys using a “delayed match to sample” task, in which the animal is trained to watch a stimulus, wait a few seconds, and then point to the remembered stimulus among several others. Some prefrontal neurons keep firing during the delay period (Fuster, 2003). Those neurons are believed to enable the momentary storage of working memory (Goldman-Rakic, 1995; see [Chapter 9](#)). This experiment isolates the temporary storage aspect of working memory.

On the other hand, selective attention experiments typically present people with two simultaneous stimuli that compete with each other. The behavior of interest is the ability to select one input over another. Experiments on conscious perception may compare conscious (reportable) to unconscious (unreportable) stimuli (see [Chapters 6](#) and [8](#)). Finally, episodic recall studies commonly ask people to recall a known event from the past. We can find distinctive brain activities for selective attention, conscious contents, working memory, and episodic recall. However, as you can see from our functional diagram ([Figure 10.6](#)), these four functions “talk to one another” most of the time. They can be isolated, but in everyday tasks they usually work together. [Figure 10.7](#) shows overlapping activation in the cortex for four mental functions that we tend to separate: working memory, attention, episodic recall, and conscious perception. The area of overlap is striking.

2.2 Using inner speech to solve problems

If you try to mentally add $3 + 5 + 11$, chances are that you can hear your own inner speech. That means you’ve recoded the figures in the previous sentence into auditory/articulatory brain activities that are partly conscious. Most people seem to have spontaneous inner speech. If we want to speak to ourselves, we do not even need a listener; we are our own audience.

We use inner speech for planning, self-reflection, and much more. It is often combined with visual imagery (as in remembering where your bicycle is parked) and probably with other “inner senses” (see [Chapter 1](#)). [Figure 10.8](#) shows brain areas that show peak activity during mental arithmetic (Wynn, 2002). Based on what you have already learned about the speech areas of the cortex, can you predict some of the active regions?

The limits of working memory must have posed difficult challenges for humans before the spread of writing. Today we can scribble notes on a piece of paper or look up information on the web. But over the neolithic ages no one wrote a shopping list before going hunting and gathering. Perhaps for that reason, spoken language gives us many tricks and tools for chunking large amounts of information into smaller packages: sentences, words, phrases, sayings, narratives, personal names, and pronouns all serve as pointers and reminders. We also condense large amounts of knowledge by named abstractions and classification schemes.

Nevertheless, even simple puzzles can show us some important features of real problems. Ideas like goals and subgoals, choice points in a problem space (see [Figure 10.2](#)), and costs and

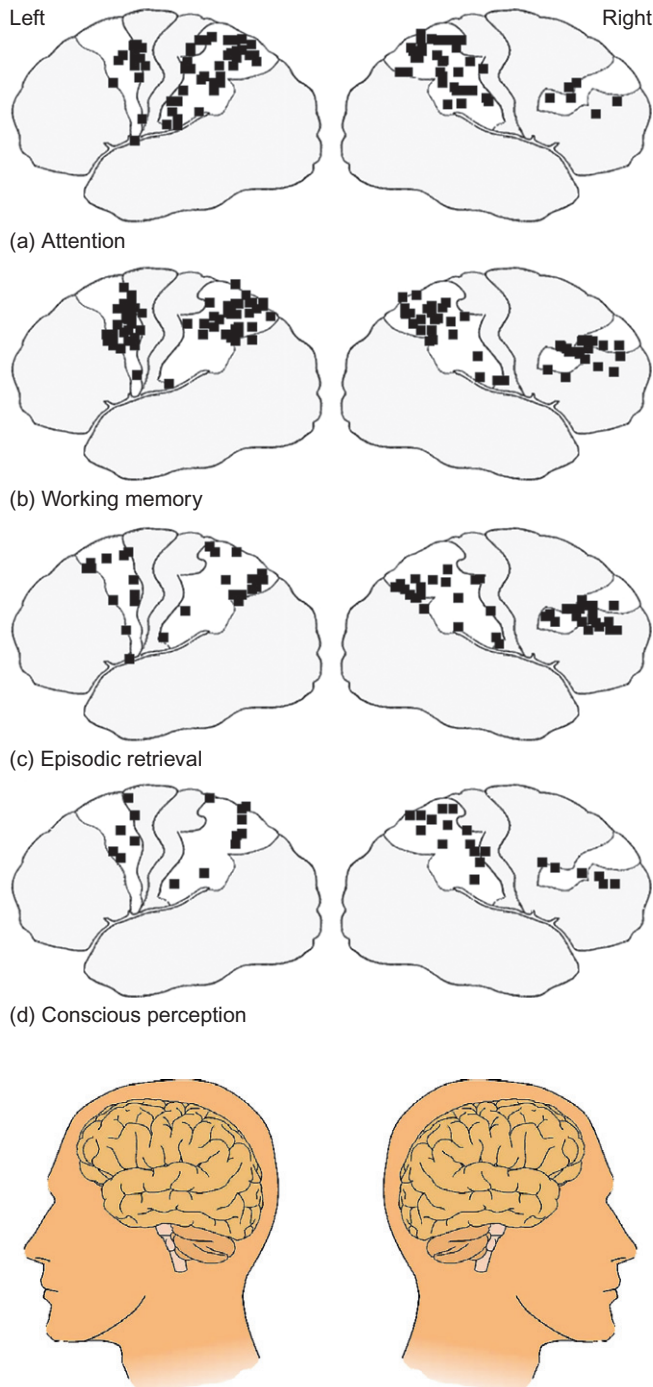


FIGURE 10.7 Overlapping brain regions support working memory, selective attention, autobiographical retrieval, and conscious perception. This figure shows schematically the widespread activation of frontal and parietal regions for four different brain activities that we often separate from one another: working memory, attention, episodic recall, and conscious perception. There is substantial overlap in these regions, and it is not obvious that they can be separated. Source: *Naghavi & Nyberg, 2005.*

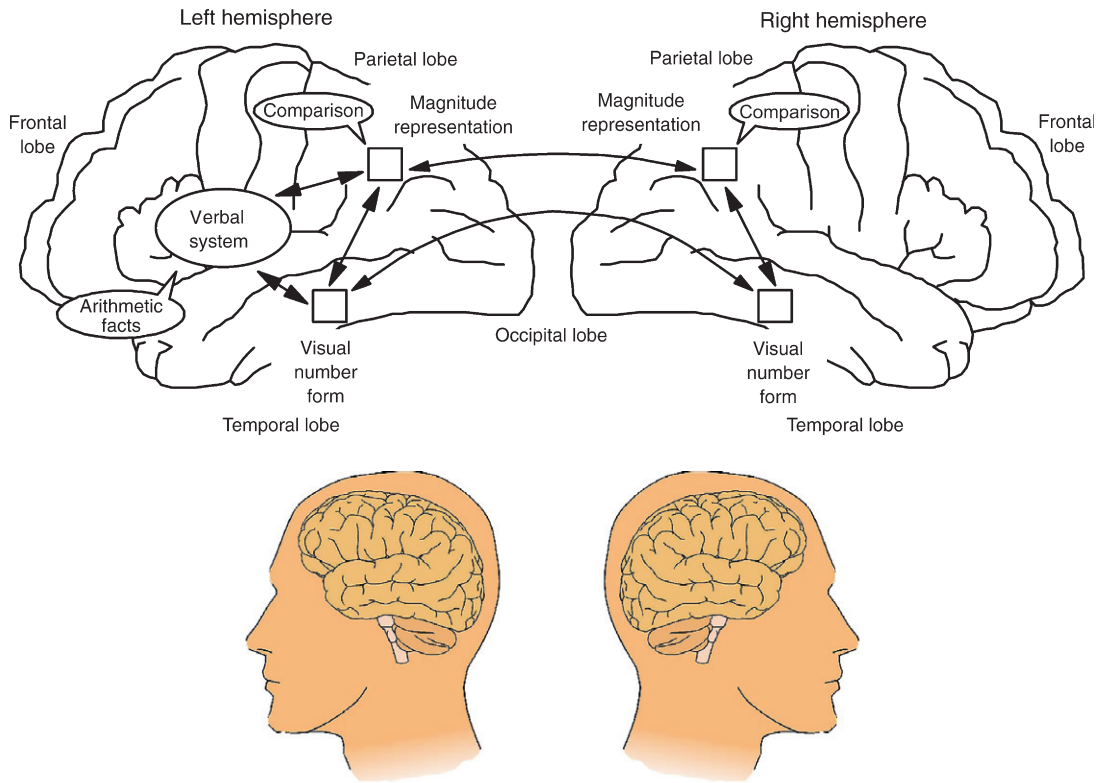


FIGURE 10.8 Mental arithmetic uses the phonological loop of inner speech. Notice the overlap in phonological tasks (such as mental rehearsal of a word list) and the subtraction task. Presumably inner speech is involved in subtraction in this case. Source: Wynn in Ramachandran, 2002.

benefits show up in many kinds of ways. While a complete problem space is rarely available for real-life problems, a useful strategy is to break down larger problem spaces into subgoals that *can* be described explicitly and completely.

2.3 Expert thinking

Much of what is known about expertise goes back to studies of chess players by De Groot (1946) and Chase and Simon (1973). De Groot demonstrated clear differences between levels of chess experts in a memory task, using brief pictures of chessboard positions taken from a tournament game. Typically, players at masters levels recalled a flashed chess picture almost perfectly, but weaker players could not remember a flashed chess board.

Chase and Simon found no difference in recall of *random* positions between three subjects: a chess master, a class A player, and a novice (Figure 10.9) It therefore seems that chess experts do *not* necessarily have better memory skills than others. Rather, chess experts recognize possible board positions, an array of pieces on the board that makes sense in a game. This result has now been repeated a number of times.

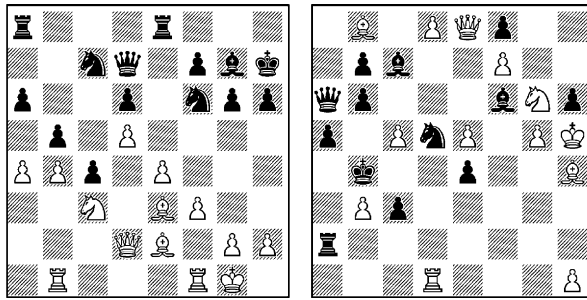


FIGURE 10.9 Types of positions typically used in chess memory research. A game position taken from a masters game (left) and a random position obtained by shuffling the piece locations of a game position (right). Source: Adapted from Gobet & Simon, 1996.

It takes thousands of hours of practice, talent, and dedication to become an expert in chess, music, or athletics. One important part of expertise is having a large and accurate set of chess patterns in memory, along with many learned tactics and strategies that may become automatic after practice. These chess patterns are chunks in the same way that the word *avatar* is a memory chunk for a virtual life player.

Working memory is crucially dependent on stored long-term information. Your understanding of this sentence depends on your memory for words, sentence structure, and meaning. Cowan (2001) and others therefore suggest that we can conceive of working memory as playing upon years of previous stored information.

2.4 Conscious goals and executive control

Box 10.2 shows a recent summary of executive control functions (Stoet & Snyder, 2009). Figure 10.10 shows cortical activation patterns for executive functions such as reasoning. Here we want to emphasize the importance of setting goals that will be pursued in flexible and persistent ways. For example, a life goal of earning a college degree can run into obstacles. Many college-age people may not be able to attend their dream college for many reasons, but there are other ways to reach the goal. Each step along the way can be considered to be a subgoal on the way to the degree. If we fail to pass too many required courses, we will not achieve the main goal. Thus goals and subgoals, flexibility, planning, outcome monitoring, and the like are natural aspects of everyday problem solving.

In addition, to reading this textbook we must both direct attention to the content of the book and *also inhibit* distracting events in the world. These are all commonsense ideas, but we now know a great deal more about their brain basis, especially the involvement of the frontal lobes. People with frontal lobe damage often have difficulty in pursuing goals, overcoming obstacles, inhibiting distractions, and switching their subgoals if necessary.

2.5 Fixedness and frontal deficits

The word *fixedness* describes the experience of being “stuck” in a way of looking at a problem that does not produce useful results. In the sciences we see some degree of fixedness whenever a major new theory or type of evidence becomes available. Pioneering scientists

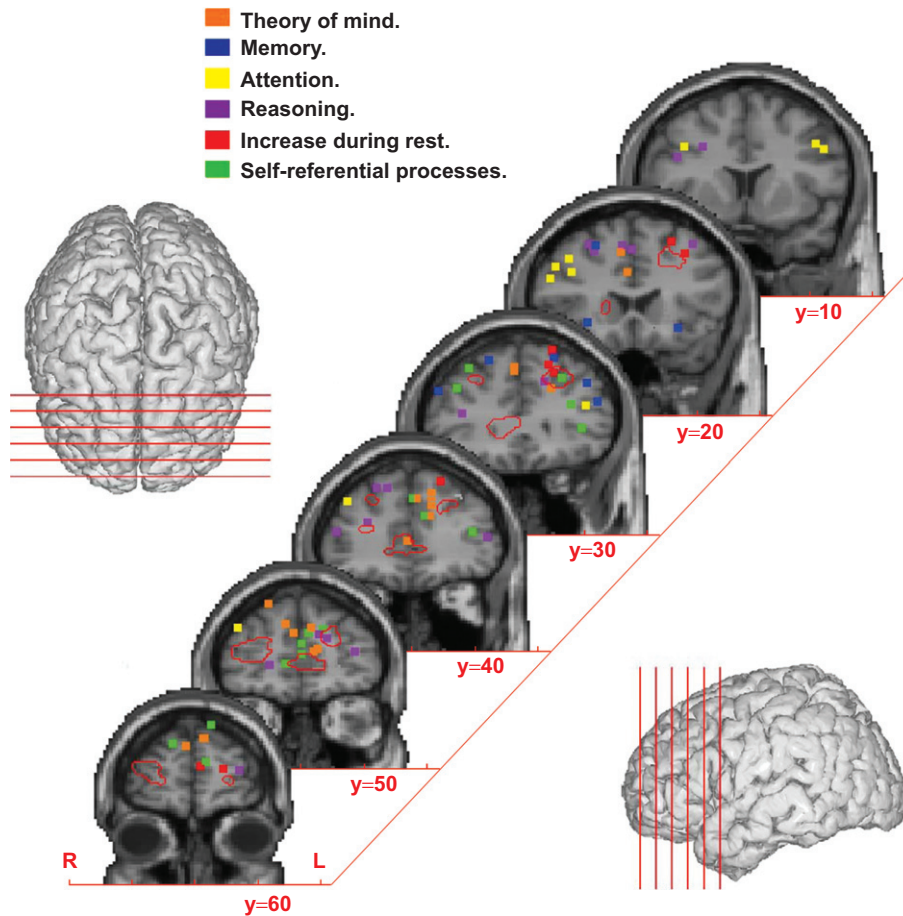


FIGURE 10.10 Some frontal capacities for high-level thinking. The frontal lobes are also needed for advanced skills, ranging from the ability to understand other people's intentions to reasoning, imagination, and self-understanding. These frontal capacities constantly interact with posterior and subcortical regions. Source: *Wicker et al., 2003b*.

like Galileo or Einstein often provoke a period of debate between old and new perspectives, but they are not immune to having their own fixed beliefs. Fixedness seems a nearly universal problem. The science fiction writer Arthur C. Clarke pointed out that many important discoveries were declared to be impossible by famous scientists shortly before they were proven to be true.

Fixedness occurs in many kinds of problem solving. It happens in chess games when one player tricks the other into making what looks like a safe move and then checkmates the opponent. Under experimental conditions it is easy to demonstrate that people can indeed become "fixated" in a habitual approach that does not lead to solutions (Duncker, 1945). In competitive games, one side can take advantage of a routine habit on the other side. Some habitual fixedness seems to be practically universal.

BOX 10.2

DEFINITIONS OF EXECUTIVE CONTROL FUNCTIONS

There are many names for *executive control functions*. These names include:

- Flexibility: the capacity to switch attention between different tasks.
- Goal setting: the capacity to set a goal that leads to effective action.
- Planning, including initiation and sequencing: the capacity to determine a series of steps necessary to reach a goal.
- Inhibiting interference: the capacity to suppress distracting or irrelevant information, thoughts, and actions.
- Monitoring: the capacity to check whether actions result in their intended outcome.
- Adjustment: the capacity to adjust a course of action in light of previous results.
- Maintenance: short-term memory for information needed to carry out executive functions. For example, to act on a goal we have to be able to keep it in short-term memory as long as it is needed to guide our actions. This may seem easy, but a large range of factors interferes directly with the ability to keep goals in mind, including alcohol intoxication, a loss of dopamine in the frontal lobes, intense emotional events that interfere with the ability to act on goals, and distractibility.

Mental flexibility, the ability to switch between different viewpoints on a problem, is associated with healthy functioning. Patients with brain damage often have difficulty solving problems because they seem to become “stuck” in ideas that don’t work.

Figure 10.11 shows the Wisconsin Card Sorting Task (WCST), which is designed to induce a misleading mental “set” in a simple card sorting task. Subjects are asked to guess which card is “correct,” using color, number, or shape. They are given feedback for each guess. Initially they are rewarded for one pattern—for example, the rule that the color yellow is always correct. At some point the rule is changed without telling the subjects. The time and number of missed trials needed for subjects to shift set are taken as an index of their ability to test different hypotheses.

Patients with impaired frontal lobes often lack cognitive flexibility and tend to score low on the WCST—they are slow to recognize rule changes and persevere in their strategy even when it is unsuccessful. Perseveration in unsuccessful strategies is also a marker of frontal lobe disorders like Alzheimer’s dementia (Ridderinkhof et al., 2002). The WCST is especially useful when frontal lobe damage is too subtle to be detected by brain scans.

Changing rules is difficult when we are mentally fatigued or drowsy or otherwise impaired. Even switching from one task to another seems to require additional mental resources beyond those involved in routine and automatic actions. Figure 10.12 shows the brain areas that are active during task switching. Refer to Figure 10.7 where we showed brain areas involved in other executive tasks. Thus drivers who are sleepy might find it harder to make fast decisions in unpredictable traffic situations, presumably because their frontal lobes may be functioning below par.

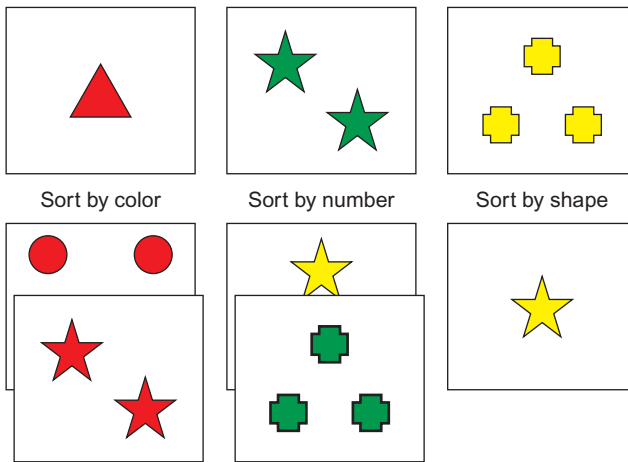


FIGURE 10.11 The Wisconsin Card Sorting Task. The WCST encourages subjects to adopt a certain rule like “the yellow color predicts correct cards.” At some point a different rule comes into play, such as *number* or *shape* of items. This is a challenge to our ability to think of alternatives to the first rule, and people with frontal lobe impairments will typically perform poorly when the rule is shifted. Source: Grant & Berg, 1993.

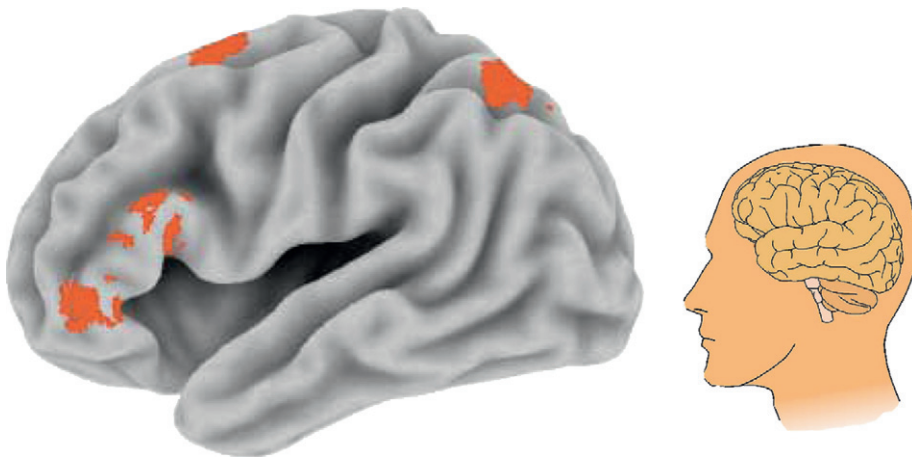


FIGURE 10.12 Task switching. Regions of high activity during task switching overlap with brain areas required in other executive tasks (see Figure 10.7). Source: Braver et al., 2003.

3.0 MENTAL EFFORT

Explicit thinking often involves mental effort—a strong sense that we are really trying hard. Mental effort has emerged in the last decade as a major variable in psychology and brain science. There seems to be a limit to the amount of mental effort we can exert each day (Baumeister et al., 2008). In the brain, different tasks that require effort show peak activity in two frontal regions: the anterior cingulate cortex (ACC) on the inside of each hemisphere

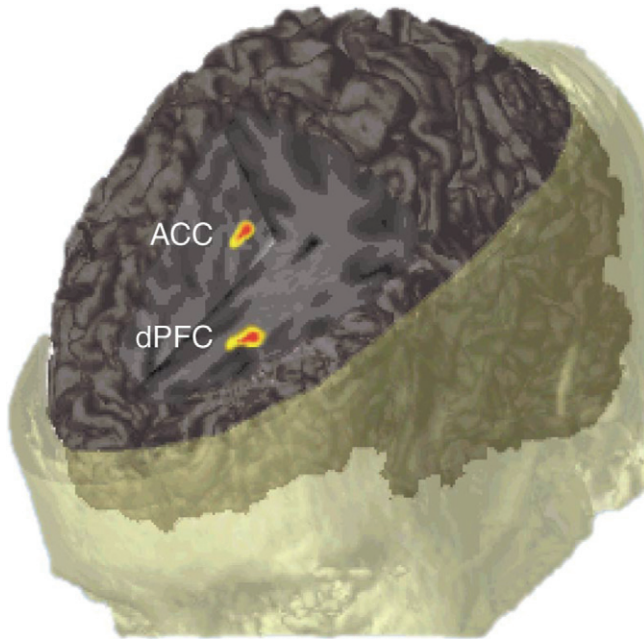


FIGURE 10.13 MacLeod and MacDonald (2000) showed that different tasks involving mental effort activate lateral and medial sides of the frontal lobe. This figure shows a 3D view of two major effort-related regions of the frontal lobe. (ACC = anterior cingulate cortex and DL-PFC = dorsolateral prefrontal cortex.) Source: MacLeod & MacDonald, 2000.

and the dorsolateral prefrontal cortex (DL-PFC) on the outside. (The “cingulate” or “belt” surrounds the corpus callosum in the inner wall of each hemisphere. “Anterior” refers to the forward half of the cingulate.)

Figure 10.13 shows two fMRI “hot spots” in each area: ACC and dl-Pfc. Figure 10.14 shows a midline view with colored squares showing where goal-related activity activates the ACC. Previous studies showed that conflict monitoring (as in the Stroop effect) evoked activity in the ACC. However, tasks as different as ambiguous emotional pictures; induced anxiety; expected, unexpected, and experienced pain; induced emotion; and expected negative pictures all showed reliable ACC activation. Other studies locate the emotional events to the forward tip of the ACC and cognitive activation, as in error detection, to the upper part of the ACC. What is new and surprising is the fundamental role of ACC and DL-PFC in many aspects of goals in problem solving. Effortful tasks also show a wider spread of brain activity, even beyond the executive regions of the frontal cortex (Figure 10.15).

3.1 Feelings of knowing

It is easy to induce a tip-of-the-tongue state. All we need to do is give people definitions of rare but known words and ask them if they feel they almost have the answer but not quite. Effective questions might include “What is the name of a vegetarian dinosaur?” or “What are two words for the technology for making artificial limbs?”

Such subjectively vague but reportable events have been found to guide intuitive problem solving, including verbal and pictorial problems; promote persistence in memory search during tip-of-the-tongue states; guide memory retrieval and persistence; and influence judgment

- Conflict monitoring
- Error detection
- Unexpected/experienced pain
- Expected/anticipated pain
- Induced anxiety
- Induced emotion (happy, sad, anger, disgust)
- Ambiguous emotion pictures
- Expected negative emotional pictures

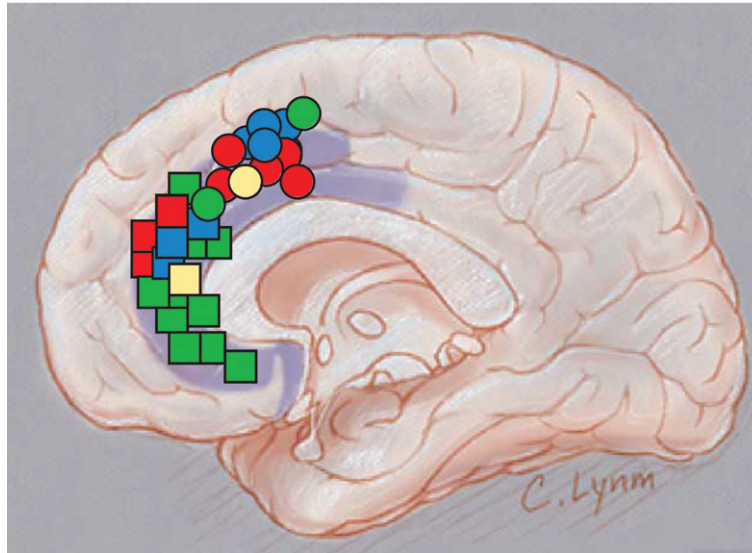


FIGURE 10.14 Error detection and resolution. This figure shows a number of different tasks, all of which activate parts of the anterior cingulate cortex (ACC). Previous studies showed that conflict monitoring (as in the Stroop effect) evoked ACC activity. However, tasks as different as ambiguous emotional pictures; induced anxiety; expected, unexpected, and experienced pain all showed reliable ACC activation. Other studies locate the emotional aspects of ACC activation to the anterior tip of the ACC and cognitive activation, as in error detection, to the upper part of the ACC. Source: Botvinick *et al.*, 2004.

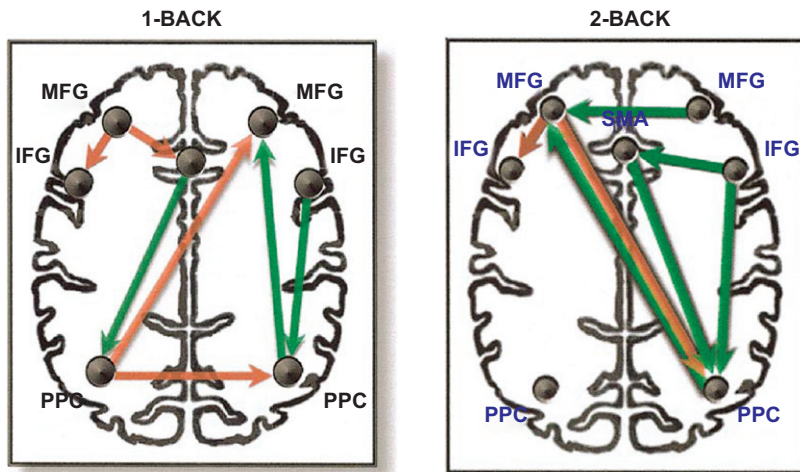


FIGURE 10.15 Connection strengths change with task difficulty. The colored lines in the brain diagrams indicate connection strengths between executive and other regions of the brain. Connection patterns change with increase in memory workload, in this case showing the connection strengths for remembering the item presented in the previous trial in a visual experiment as compared to remembering the item presented two trials previously – which increases the mental (memory) workload. Source: Honey *et al.*, 2002.

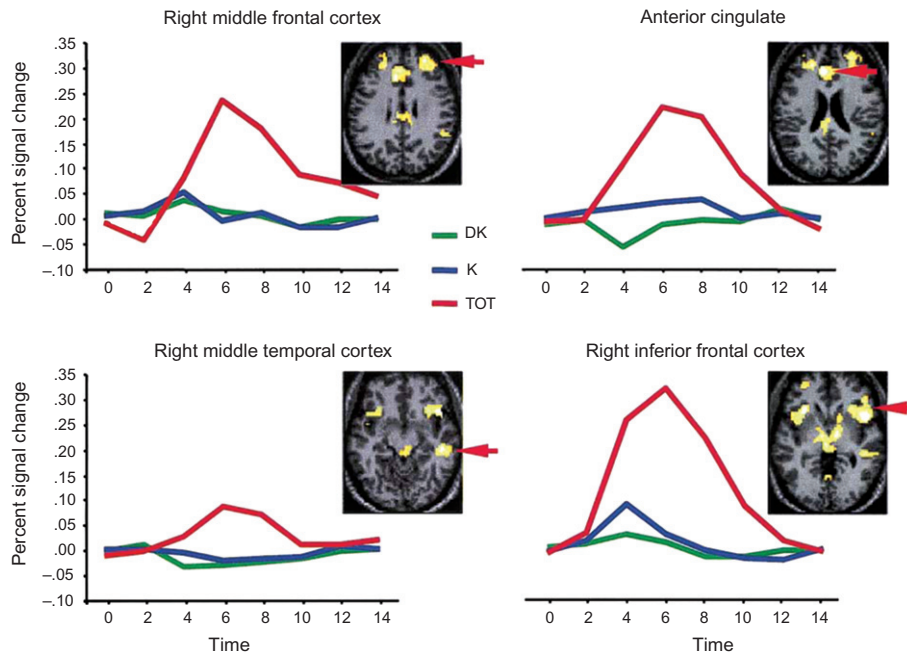


FIGURE 10.16 Effortful thought in word finding. These figures show both the location of the increased activity in the “tip-of-the-tongue” state and their time course (using event-related potentials). Notice that the classical executive regions are again active. While these regions are not normally viewed as contributing to conscious experience, the fact that tip-of-the-tongue states can be reported in a verifiable manner suggests that they are at least “fringe” conscious. Abbreviations: DK = Don’t Know, K = Know, TOT = Tip of the Tongue. Source: *Maril et al., 2001*.

tasks and decision making. Maril and colleagues (2001) have shown that the tip-of-the-tongue state (shown in the red lines in Figure 10.16) showed high activity in temporal and frontal regions, the same cortical areas that are associated with persistence in problem solving.

4.0 CONCEPTS

Abstract concepts are some of our most powerful thinking tools. That is especially true in science and technology and in academic disciplines. However, in daily life we may use a number of shortcuts. One important example is “perceptual symbol systems” (Barsalou, 1999), the use of concrete images to stand for abstract ideas.

4.1 Sensory images can stand for concepts

Intuitively, we tend to have some misleading ideas about human cognition. One is that we carry pictures in our heads that represent the world around us. The evidence suggests instead that we tend to use visual images that are prototypical reminders of categories in the world, rather than accurate images of categories like chairs and movie stars. We seem to have a

network of perceptual, cognitive, and motoric knowledge about chairs and their uses. Such networks can be accessed by prototypical pictures of chairs ([Figure 10.17](#)).

Humans have a preference for such prototypical images, but they are not accurate depictions of all the chairs we have ever known (Barsalou, 1999; Rosch, 1975). Rather, they are special members of a category—of chairs or movie stars—that stand for the entire category. The wooden chair in [Figure 10.17](#) may not be the average chair you have seen. But that visual image might come to mind more easily than the plastic or metal chairs we tend to see more often.

Barsalou (1999, 2005) has suggested that we have a strong perceptual bias, even in dealing with abstract categories. One reason is that we do not come into the world with an understanding of abstractions. The early years of childhood are devoted to sensory, motor, and emotional exploration of our surroundings. From an adult point of view, young children are very involved with the sensorimotor world. When we get older, we may not lose that early foundation in sensation, perception, emotion, and actions. We may simply use perceptual symbols that are anchored in childhood experiences but that we now think about as abstractions.

4.2 Knowledge and networks

Another intuition is that common words and concepts are simple because they often have simple names like “car,” “brain,” and “person.” This intuition is also very misleading. Mental representations, including words, visual images, and concepts, should be viewed in terms of elaborate networks of knowledge. The cognitive evidence for such networks was extensive even before the advent of brain imaging methods. It can indeed be found in the study of the development of scientific concepts themselves. There are no single, isolated concepts like “gravity”; there are only networks of concepts and facts that together help to make sense of the word “gravity” (Kuhn, 1962).

Naively, we tend to think of basic scientific ideas like “gravity” and “molecule” as single ideas. Some philosophers therefore proposed that there must be a one-to-one relationship between the Newtonian concept of force and the physical observations that gave rise to that concept. But others pointed out that there is no observable correlate of Newtonian force at all; we only measure mass and acceleration. “Force” is a purely inferential concept in physics (see [Chapter 1](#)). Newtonian theory is not just a list of concepts but a network of carefully defined ideas supported by standard experiments, by predictable observations, and tied into a web of mathematical inferences. Scientific theories are therefore semantic *networks*, not just labeled collections of observations. The same argument applies to the words of natural language.

These points are fundamental for understanding how the brain represents knowledge. In brain imaging we rarely see abstract classes of objects. Rather, we see perceptual objects in sensory regions of the brain, which gradually shade into more abstract forms of representation. Ideas appear to be represented in the cortex in terms of complex webs of learned connectivities, rather than localized filing systems with neatly arranged conceptual categories. The brain is a very practical organ, always close to the sensorimotor and motivational world, rather than being an abstract logic machine. (The brain can do logic, of course, but most of the time it is focused on more down-to-earth problems.)

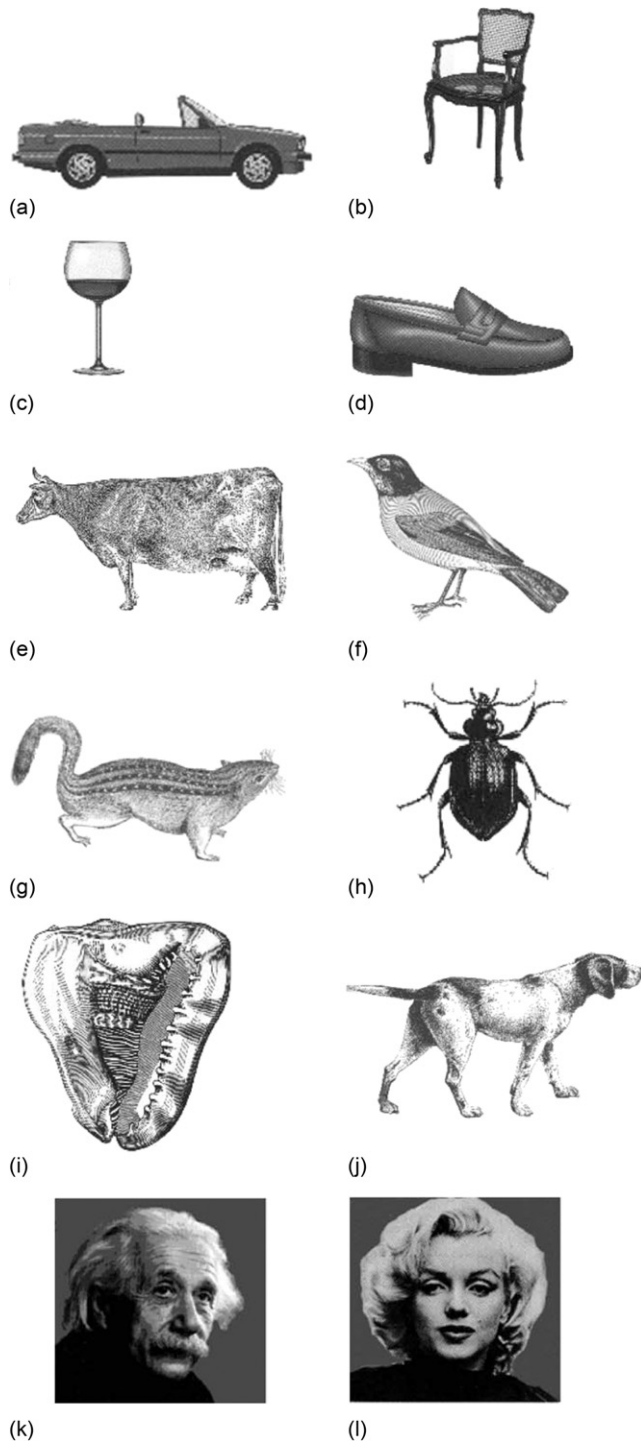


FIGURE 10.17 Visual prototypes tend to stand for more abstract categories. Source: *Laeng et al., 2003*.

5.0 IMPLICIT THINKING

People cannot tell us about their unconscious thoughts. To study implicit cognition we can watch what people do, but their reports may be inconsistent with their actions. What people tell us may be what they *think* they are doing. Reliable studies of implicit problem solving are therefore fairly recent.

However, implicit problem solving may happen more often than the explicit kind. Soon after birth we start learning new skills. Babies babble spontaneously. Childhood play helps to practice eye-hand coordination, social and emotional habits, and learning our own limitations. By age 10 we have many overlearned skills that are largely unconscious.

In general, implicit thinking involves the following:

1. Less executive control and decision making
2. Less conscious involvement
3. Less mental effort
4. Less metabolic activity in the brain, as measured by fMRI, EEG/MEG, or direct brain recording

Speaking, listening, writing, and reading are mostly implicit. We use them without even knowing what we are doing. In reading the last sentence you were probably unconscious about your own eye movements. Eye movements in reading are not random but very selective and purposeful. Moving your eyes in reading involves fast and highly skilled problem solving.

Expert readers may be unaware of entire levels of language processing, like word identification, phrase comprehension, syntax, and semantics—processes that we may use every second (see [Chapter 11](#)). There are many ways to disrupt practiced skills, thereby turning implicit routines into explicit thinking. We can make words harder to perceive by crossing out letters, scrambling their order, or making their meanings harder to understand. ~~Notice that you have to pay more effortful attention when these letters are crossed out.~~

Implicit problem solving takes less executive control than explicit thinking: it involves less conscious access, less subjective effort, and less cortical activation in fMRI studies. Implicit thinking depends more on long-term memory and highly practiced routines. Consistent practice and rehearsal can turn explicit problem solving into the implicit kind.

We have touched on the ways in which novel skills become unconscious with practice. In addition, humans seem to have very little conscious access to subcortical events, like the workings of the cerebellum. Some activities in visual cortex are reportable with very high accuracy, just as you can report the words and letters on this page, but the “dorsal stream” of visual cortex seems to be inherently unconscious (Milner & Goodale, 1995). Even after 50 years of research, we are only beginning to understand the brain basis of conscious compared to unconscious cognition.

In the last decade or two, the evidence has grown for implicit routines in semantic inferences, in some sensory events, interpersonal biases, goals, and emotions, and even for implicit working memory. Brain imaging gives us a tool for studying events that people may not be able to tell us about. Even some goals and motivations are now believed to be implicit (Greenwald & Banaji, 1995).

6.0 SUMMARY

Working memory is the domain of explicit problem solving. However, completely explicit problem solving is quite rare in the natural world. While implicit thinking is efficient, it is also vulnerable to rigidity and difficulty in controlling the details of what we are doing. An optimal problem-solving strategy mixes explicit and implicit approaches. Fringe-conscious judgments are commonly encountered in tasks like “feelings of knowing” and the “tip-of-the-tongue.” These tasks may give us *metacognitive* knowledge about ongoing implicit problem-solving processes. They are believed to activate the executive regions of the prefrontal cortex.

7.0 STUDY QUESTIONS

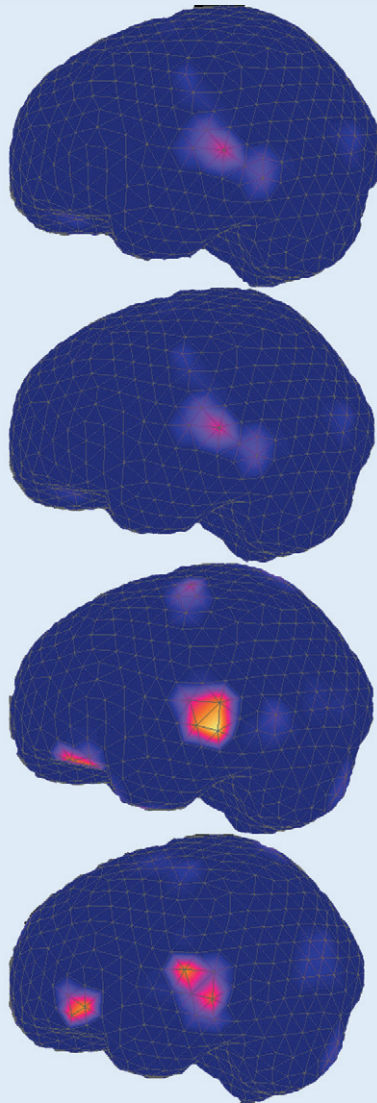
1. What are the major features of explicit problem solving? Implicit? What brain differences can we expect?
2. How does expert thinking in chess differ from novices?
3. Give an example of “chunking” in an expert task. Why is it useful in problem solving?
4. What brain changes occur when people learn a balancing task? What are the implications for problem solving in the real world?
5. What brain regions may be impaired when our ability to solve problems decreases? What are some possible causes?

Language

O U T L I N E

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When the patient was admitted ... at the age of 21 ... he could no longer pronounce more than a single syllable... ; whenever a question was asked of him, he would always reply "tan, tan."... *Pierre Paul Broca* (1861b)



The MEG recording of the cortical response to a single spoken word, from the top panel downward, showing a fast-spreading wave to an unexpected stimulus.

Source: *Pulvermüller et al., 2006.*

1.0 INTRODUCTION

Language is the foremost tool of human thought and culture. It is also one of the major landmarks of child development. Before our fourth birthday, we understand the phonemes of our first language, our basic words and grammar. New words are learned at a very fast pace during those years. Young children use their early language to reach important goals (Figure 11.1). Even before they learn language, they have a good basic understanding of the world around them.

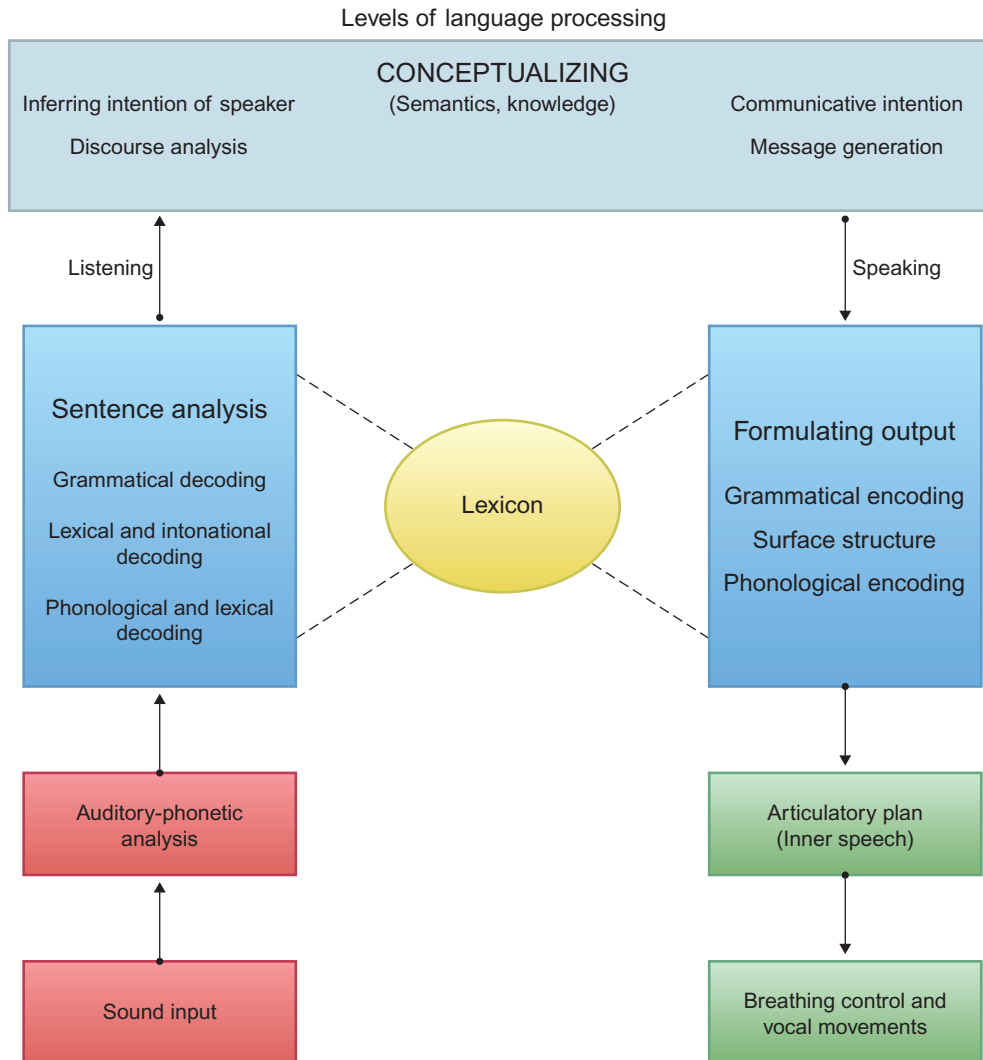


FIGURE 11.1 Levels of language—listening and speaking. A sketch of levels of language analysis and production. Each level is highly complex but is processed when we become skilled speakers. Source: Baars, adapted from Miller, 1991.

It is interesting to ask someone to repeat a sentence he or she has just heard. A few seconds after hearing it, most people cannot repeat the actual sentence, but they will remember the *gist*—the meaning of the sentence (Sachs, 1967). As soon we understand the specific words, we tend to forget them.

Within a few seconds, the speech sounds we hear therefore go through the following steps:

1. Sound analysis—turning sounds into phonemes and syllables
2. Word identification—recognizing the words we know
3. Grammar—identifying nouns, verbs, and phrases
4. Semantics—accessing a network of meanings
5. Discourse—how do the meanings relate to previous ones in the conversation?
6. Purposes—what is the speaker’s goal, and what does it mean for me?

2.0 THE NATURE OF LANGUAGE

Human beings are biologically specialized to produce and hear speech. But full-blown language is believed to go back “only” 100,000 to 200,000 years, when ancient cultures started to accelerate the use of spoken and crafted symbols. Symbolic objects like grave decorations, small sculptures, body decoration, bone flutes, bows and arrows, cooperative hunting, and much more are believed to have grown up together with language. Human settlements go back about 16,000 years, and the first great city-states and empires go back 6,000 years. About 2,500 years ago the first practical writings systems spread around Asia and the Middle East, leading to our earliest records of ancient civilizations from Egypt, Sumer, India, China, to Greece and the Levant, the lands of Israel and Palestine. Modern science and technology took off about 500 years ago, with steel and steam power coming 200 years ago. Modern medicine only dates back a century or so. Radio, television, computers, the web, and biotechnology go back a half century. Brain imaging technology is only a few decades old.

2.1 The biology of language

Children learn language in predictable stages, and they even make up their own “creoles”—true languages—when they grow up in mixed-language communities (see [Box 11.1](#)). Spoken language evolved over existing vocal and auditory physiology. Speech *output* tends to be run by the left hemisphere, but early brain damage can shift it to the right side (see [Chapter 1](#)).

“Language cortex” has only become specialized during hominin evolution—less than 3 million years out of the 200 million years of mammalian evolution. Prior to hominins, Broca’s area was involved with vocal tract control for such roles as reptilian threat sounds. It is located next to the mouth and tongue cortex of the motor homunculus. The working vocabulary of living languages has expanded in recent history, but our grammar actually may be simpler than ancient languages.

Speech and language involve biological preparedness in much the same way that manual dexterity, vision, brain development, and social relations do. Genetics always interacts with life experience. Which language we learn in childhood—the words, meanings, and much

BOX 11.1

CREOLE LANGUAGES ARE SPONTANEOUSLY
MADE BY CHILDREN

Creoles are languages with simple syntactic structures that develop when adults who speak different languages live in the same area and need a way to communicate. The adults in such situations make do with a simple communication system with a limited number of nouns, verbs, and modifiers combined with gesturing. Children growing up in multilingual communities often learn their parents' language; more important, they also create a *creole*, a true language. Creoles have

common features, similar to fully developed languages. Thus, the children in multiple-language communities can develop a more full-fledged language than their parents.

Bickerton (1984, 1990) points out that, in many cases, the features of creoles are not present in the languages spoken by the parents. Therefore, creoles are likely to be innately specified. Creoles may reveal what features of language develop most easily. These features may arise in languages at an early stage.

else—depends on our experiences. Our cultural and personal achievements are partly dependent on our biological gifts.

Figure 11.2 shows the classical understanding of Broca's area for speech production and Wernicke's area for speech perception and comprehension. Physicians in the nineteenth century discovered a number of other aphasia (language deficits). The best known of these is conduction aphasia, which is associated with the large bundle of axons that connect Broca's and Wernicke's areas (Catani & Ffytche, 2005).

Broca's area is now believed to have many more functions than speech production. As neuroimaging reveals smaller and smaller functional language regions in the cortex, new roles of the left inferior frontal gyrus (LIFG) are constantly being found. The cortex has about a thousand specialized regions (starting from about a hundred Brodmann areas from 1905). Each patch of cortex is an active set of processors, intimately connected with its neighbors

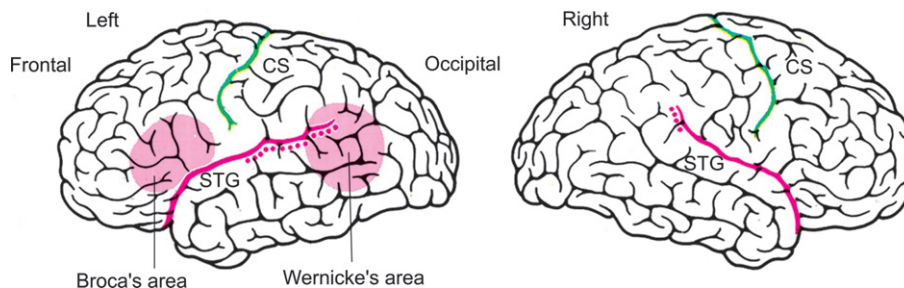


FIGURE 11.2 Wernicke's area is near the auditory cortex. Broca's area is next to the mouth and vocal regions of the motor cortex. The location of these areas in those neighborhoods makes functional sense. Source: Standring, 2005.

and with distant specialized areas through the long axonal networks of the white matter. This active highway system looks more like the World Wide Web than a simple flowchart.

We can use words to evoke mental images, like a coffee cup or a favorite picture. We can describe a beautiful song in words, or at least try to. We can have thoughts even without speaking out loud. Language is therefore not a single, fixed skill. Figure 11.3 sums up more than 125 brain imaging experiments, showing more than 700 speech-related activity peaks in the left hemisphere. (Vigneau et al., 2006). Language is not a single activity.

However, there are some basic findings. Figure 11.4 shows constant looping between the sensory and motor parts of cortex. Some scientists, like Hagoort (2005), believe that Broca's area (see Figure 11.2) should be expanded to include the gray oval area in Figure 11.5, which may *unify* speech sounds, meanings, and grammar. This "unification area" might include

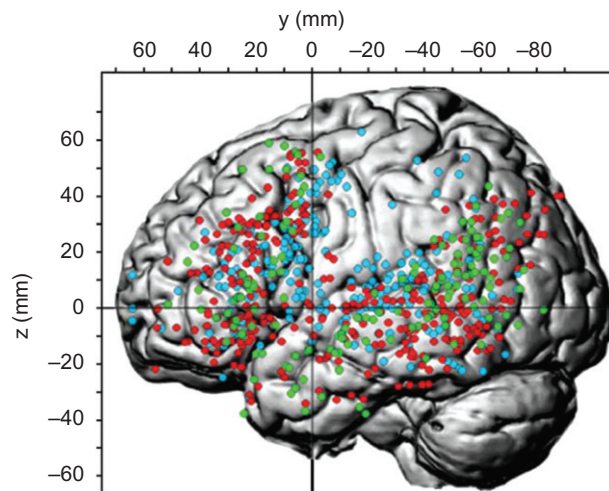


FIGURE 11.3 A summary of more than 100 brain imaging experiments, showing 730 activity peaks (Vigneau et al., 2006). The blue points show peaks for the sounds of speech. Red regions show semantics—the meanings of words and phrases—and the green dots show sentences and text. The three colors overlap a great deal. Source: Vigneau et al., 2006.

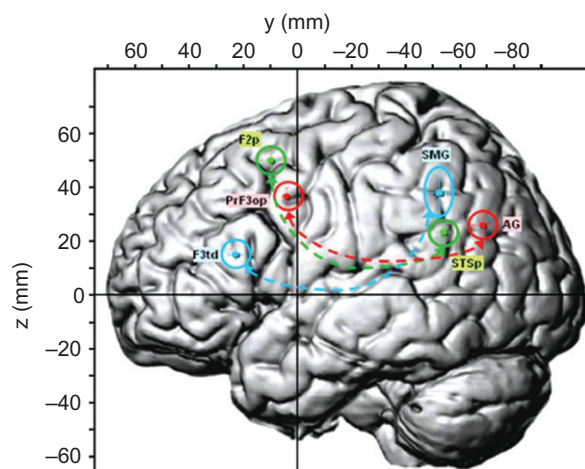


FIGURE 11.4 Working memory for phonology, semantics, and sentences connects posterior hearing areas to frontal speaking areas. Source: Vigneau et al., 2006.

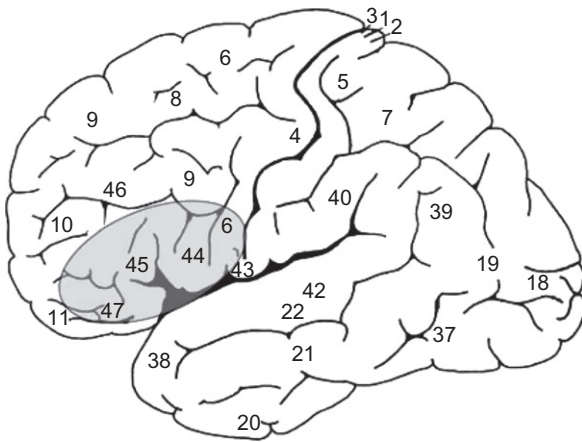


FIGURE 11.5 An expanded concept of Broca's area. The left inferior frontal gyrus (LIFG) is a better label for the area involved in speech planning and production (LIFG is sometimes considered to include areas 6, 44, 45, and 47 of the left hemisphere). Hagoort (2005) suggests that LIFG is a unification zone for speech, a place where different features of spoken language are combined before being sent to the motor cortex. Source: *Hagoort, 2005*.

memory links with the temporal lobe and executive functions from the prefrontal cortex (dorso-lateral-prefrontal, i.e., upward, to the side, and in front of the motor cortex). Language is not limited to the left hemisphere. It expands like some vast metropolis into the nonspeaking hemisphere. For many functions the two hemispheres are thoroughly integrated.

2.2 Language origins

If children grew up without language, would they invent their own? In fact, in isolated communities like small islands, adult speakers of different languages may settle in the same place. Adults rarely learn a new “accent” (phonology) or grammar. Instead, they tend to speak a mixed version of the two languages, a mixture that is good enough to talk with other adults, but without the fluency and richness of their first languages. Children in bicultural communities may develop a language of their own, now called a “creole” because they were first studied in the Creole communities of the Caribbean Islands (see [Box 11.1](#)) (Bickerton, 1984, 1990). Creoles are organized like normal languages, with their own phonology and grammar. It therefore seems that children do carry the basic capacity to create full-fledged language.

2.3 Speech versus language

Right now you are using your eyes to read. You have learned to read, write, and type with remarkable facility. You could learn sign language, Braille, and symbol systems like mathematics, logic, and computer programming. Thus, language can extend beyond pure speaking and listening. The great majority of children learn spoken language in the first years of life, but reading and writing come later and have a lower rate of success. We therefore seem to have a special talent for spoken and heard language, but with effort and skill we can expand our biological skills into new domains.

3.0 SPEAKING

The human vocal tract is basically a tube with two flaps just above the lungs and its diaphragm muscles, which pump out air (Figure 11.6). The vocal tract is much like a saxophone, with the reed vibrating at the top of the tube. Our vocal flaps can vibrate faster or slower, producing higher or lower pitches. We make consonants by squeezing the vocal tube in the back, the middle, or the front of the tube. In English we use the lips for /b/, /p/, and /m/, the tongue against the top of the mouth to make /g/, /k/, /ng/, /r/, and the teeth in the front for /th/, /the/, /s/, /z/, /v/, /w/. If we stop the flow of air completely, we make no sound at all. The stop consonants like /b/, /p/, /t/, /d/, /k/, /g/ only make transitional

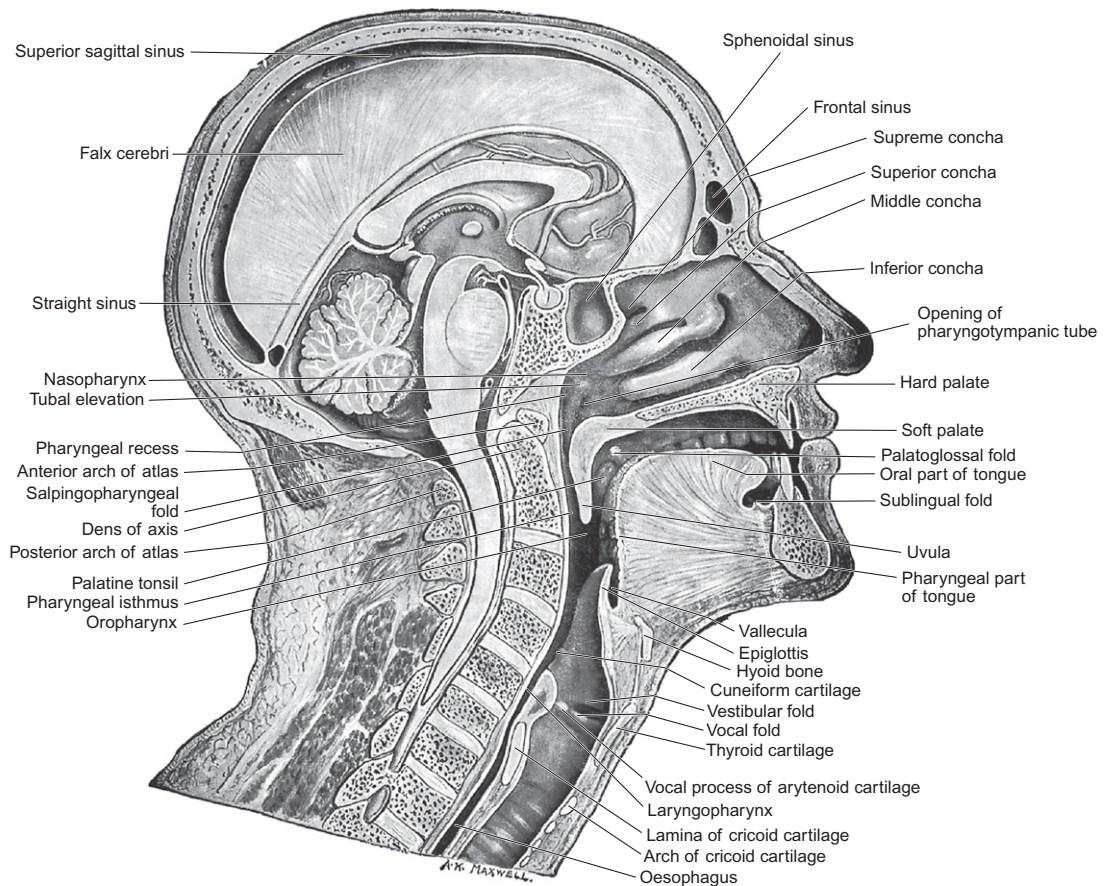


FIGURE 11.6 The human vocal tract uses mechanisms inherited from ancestral species. The vocal tract is a tube, with a source of tuned turbulence from the vocal cords, two flaps of tissue in the larynx. The quality of vocal sounds results from resonance between resonant spaces and surfaces throughout the head and torso. While consonants squeeze or close the air tube, vowels are shaped by holding the tongue and lips to make a musical note. Difference vowels change resonant frequencies of the vocal tract. Vowels and consonant-vowel syllables are used by all languages because of the physics of tubes and air vibrations. Source: *Standring, 2005*.

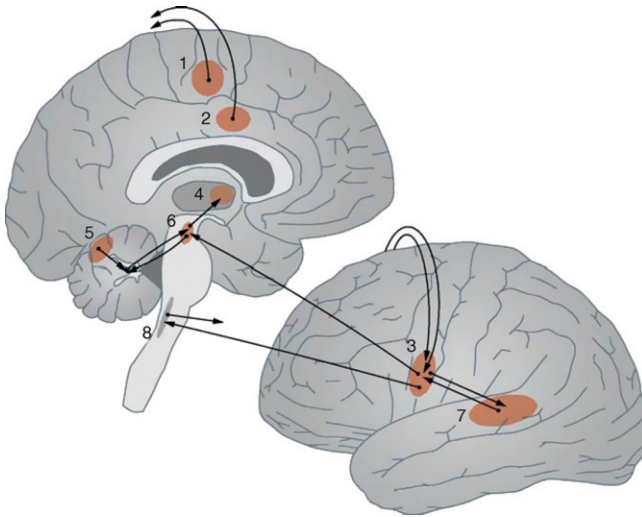


FIGURE 11.7 Pathways between speaking and hearing. In the left hemisphere you can see the classical axon bundle running between Broca's and Wernicke's areas. However, there is signaling between the hemispheres as well (the right hemisphere can understand spoken language), as well as links to specialized regions below the cortex, including the thalamus, brainstem and cerebellum. Source: Parker et al., 2005.

sounds when we close for the phoneme /k/, for example, and then open it for /i/ as in the word “key.” Other languages shape the air flow in different ways, but the physics of sound production is similar. Click languages have a very unusual set of skills for stopping the flow of air, including the English sound that’s spelled “tsk, tsk, tsk.” The vocal tract is a very creative organ, as you can tell when listening to a great singer or storyteller.

Sound vibrations echo through the head and body, oscillating all the soft tissues and air cavities. By holding one’s nose, one can change the quality of the voice. Those vibrating, air-filled body cavities also allow us to tell the difference between voices. Children’s voices sound higher than adults’ because they have smaller vibrating cavities.

Singing is prolonged speaking: We stretch out the vowels and tune them to a specific pitch. But even ordinary speech has a kind of melodic phrasing called *intonation*. In English, a question intonation raises the pitch of the last syllables of a phrase. A vast range of emotions are expressed by the intonations of speech.

Musical rhythm resembles spoken stress patterns, as in poetry and rap music, for example. Therefore singing, speech, rhythm, and emotional expressions use the same voice instrument. Cortical regions for speech are closely associated with audition (for sensory input) and with mouth and vocal tract representation (on the output side) (Figure 11.7).

4.0 WORDS AND MEANINGS

English is a member of the Indo-European language family. This family includes Persian and a number of languages spoken on the Indian subcontinent. Other language families make quite different choices for pronunciation, word order, and the like. Finnish and Turkic languages string morphemes into long utterances, like the unusually long English word “anti-disestablishmentarianism.” Tonal languages like Chinese and Tibetan take the opposite

approach, compounding sentences from short words, modulated by a rich melodic shaping of each syllable, so a word like “Chang” can mean different things depending on its tonal contour. Still, all languages have wordlike units of some kind. As Figure 11.1 shows, language may be viewed as a double hierarchy, going from sound to meaning on the input side and from meaning to vocal movements in output.

4.1 A cultural treasury of words and ideas

Words are the basic building blocks of meaning. However, sentences can be taken as basic “meaning formulas,” like mathematical formulas. We often think and communicate in sentences that express a meaningful proposition of some kind.

The words of natural language give us a great legacy of useful meanings, developed over centuries. In many cases, we can trace word origins more than a thousand years. A nice example is the word *quality*, which is derived from the Latin translation (by the Roman writer Cicero) of the ancient Greek expression “po io tes,” or “what is it-ness.” Cicero apparently found “po io tes” in a famous dialogue by Plato featuring his teacher Socrates and translated it into the Latin word *qualitas*. Before *qualitas* became popular, European languages had no way to refer to the “what is it-ness” of a sound, a taste, or any other category of events. A single vocabulary word like “quality” allows us to treat a concept as a single chunk in working memory. In science, terms like *DNA*, *bit*, *computer*, and *brain imaging* allow us to chunk complicated concepts into a few words and thereby create a whole new semantic space of reference.

Roget’s Thesaurus, first compiled by Peter Mark Roget (1779–1869), is one historic effort to classify a natural language into semantic categories. Modern efforts use computational methods, but characterizing our knowledge of basic concepts is still an awesome enterprise. George A. Miller’s WordNet system at Princeton University, an online lexical reference system, is a modern Roget’s Thesaurus (<http://wordnet.princeton.edu/>). Over a period of years, it has classified more than 200,000 pairs of words and meanings in English. Similar efforts are under way in other languages. WordNet counts about 128,000 single-meaning words and about 80,000 words with multiple meanings. However, this does not include words with multiple syntactic roles, like *book*, which is both a noun and a verb (as in “booking a ticket for a flight”). *Book* also can also play the role of an adjective (as in book-learning, bookbinding, a bookish person). The number of words and meanings in language is enormous. It is one of the basic treasures we inherit from our cultures.

5.0 SYNTAX AND SEQUENCING

Syntax is a distinctive aspect of language, involving sequencing of syllables and words. Figure 11.8 shows a syntactic tree with a subordinate clause. Tree structures can embed phrases within phrases. This is a specialized skill that is different from understanding the meaning of a single word. Figure 11.9 shows brain regions that support syntactic processing.

Syntax gives us a way to plan a sentence in much the same way we plan other actions—like navigating from one place to another. Syntax can be seen as a planning tool (see Chapter 10).

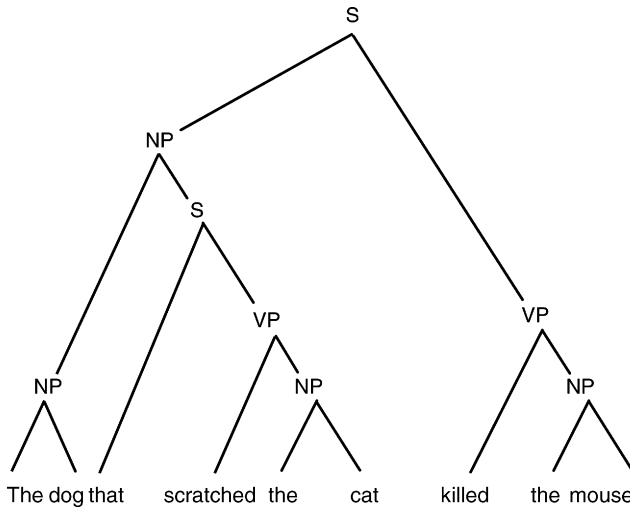


FIGURE 11.8 Syntactic “tree structures” can have phrases within phrases. A basic syntactic tree, containing an embedded clause. Source: Gitelman et al., 2005.

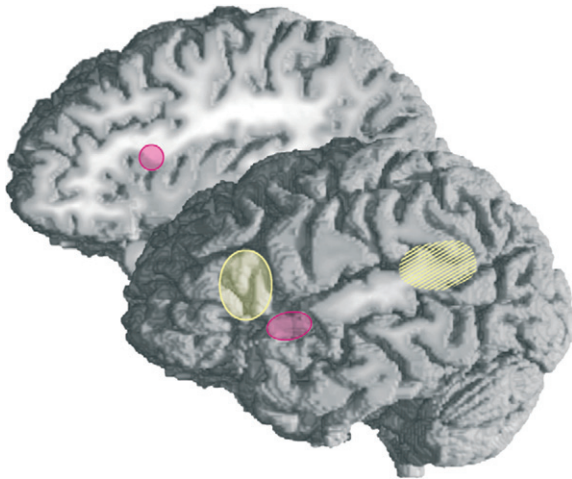


FIGURE 11.9 Syntax evokes distinctive brain regions. Grodzinsky and Friederici (2006) suggest that different cortical regions support different syntactic functions. Source: Grodzinsky & Friederici, 2006.

6.0 SPEECH AND MELODY

Speaking and singing are similar. Physically, singing is just a lengthening and tuning of vowels. If you stretch out the vowels of the words “cognitive neuroscience,” you are already singing in a monotone. Then you can change the pitch of each syllable, and you have a little song. Like language, music and dance are species-specific capacities in humans. Other living primates do not have those specific skills, though they certainly share a great deal of semantic knowledge with us.

Some sort of musical scale is used in many different cultures. All musical cultures divide up the octave. Musical notes, like the vowels of language, are based on the physics of resonant tubes, like bone flutes or the “twang!” of a bowstring. When the vibrating column of air in a

flute is half as long, the sound will be an octave higher. When a guitar string is twice as tight, it is also heard as the same note an octave up. Thus, there is a physical basis for pitch perception. It makes more sense to run away if you hear the roar of a lion than the chirp of a cricket, because big lungs that squeeze air through big cavities make loud and low sounds. We can therefore guess at the size of an animal just by hearing it.

Depressed people tend to show a declining intonation contour, perhaps reflecting a lower level of air pressure. Joy is often expressed with upward swoops of sound. Emotional expression may precede and later coevolve with language. Different musical intervals—that is, two-tone sequences—seem to have different emotional meanings.

Even rhythm is an aspect of speech, as we can see in the stress pattern of spoken sentences: “The *rain*/ in *Spain*/ falls *mainly*/ in the *plain*/.” You can mark the stressed syllables in any

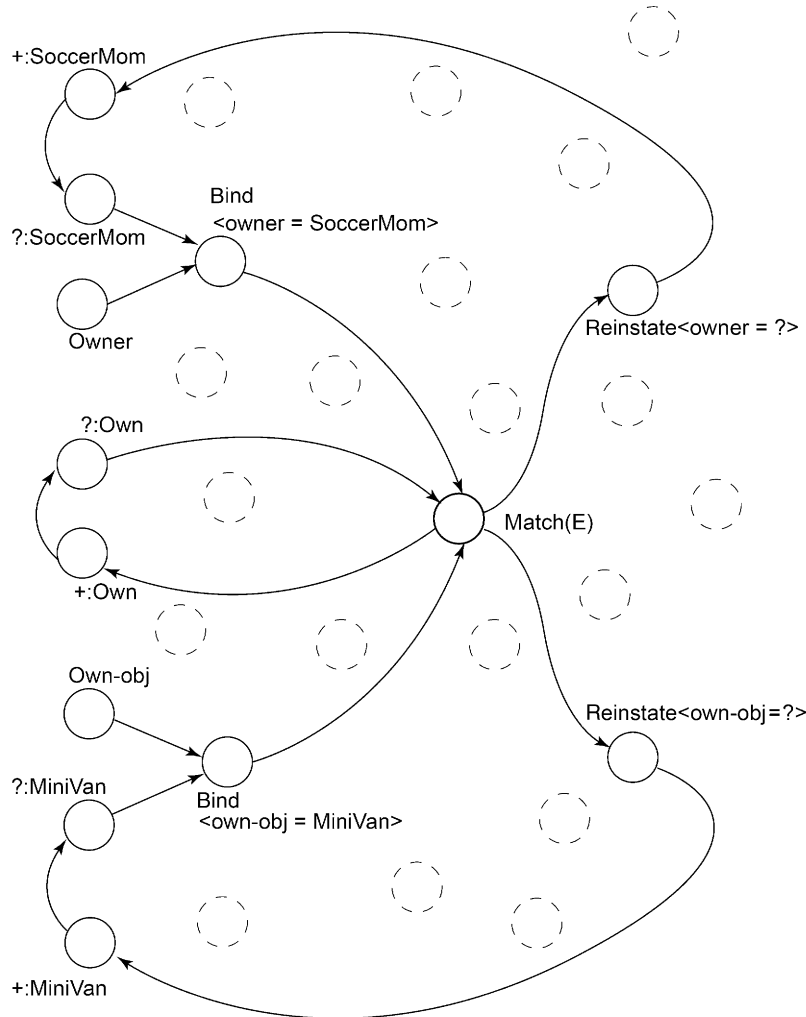


FIGURE 11.10 A proposition may involve a distributed neuronal network. In the cortex the proposition “Soccer moms are likely to own minivans” can be shown by a collection of neural activities for the parts of the sentence: *minivans*, *moms*, *soccer*, *owner of*, and the like. Such networks have not yet been observed in the brain. Source: *Shastri*, 2002.

sentence. Babies spontaneously babble in a singsong, and adults spontaneously speak to children (and pets) using exaggerated intonation. While different cultures have different musical forms, it seems that there are universal links between language and music.

7.0 MEANING

We do not speak in single words but in propositions—that is, in semantically meaningful sentences. Syntax makes it possible to state propositions. But even aphasic (nonlanguage) patients may point to desired food, express discomfort and pleasure, and use gestures to communicate with other people. Figure 11.10 gives an idea of how different neurons might express different parts of a proposition. By combining these neuronal activities, propositions might be coded in the brain.

8.0 THOUGHTS BEFORE LANGUAGE

Speaking often seems to start with a goal to express a certain meaning. The meaning of a thought may then turn into different levels of description: semantic, syntactic, phonemic, vocal, pragmatic (i.e., personal goals), and more. Once this many-layered tower of brain planning is ready, it could begin to give vocal commands to move the vocal tract.

Figure 11.11 shows this basic idea. Notice that there are overlapping levels, each perhaps reflected in a set of neural arrays. In the figure, each level is associated with a different part of

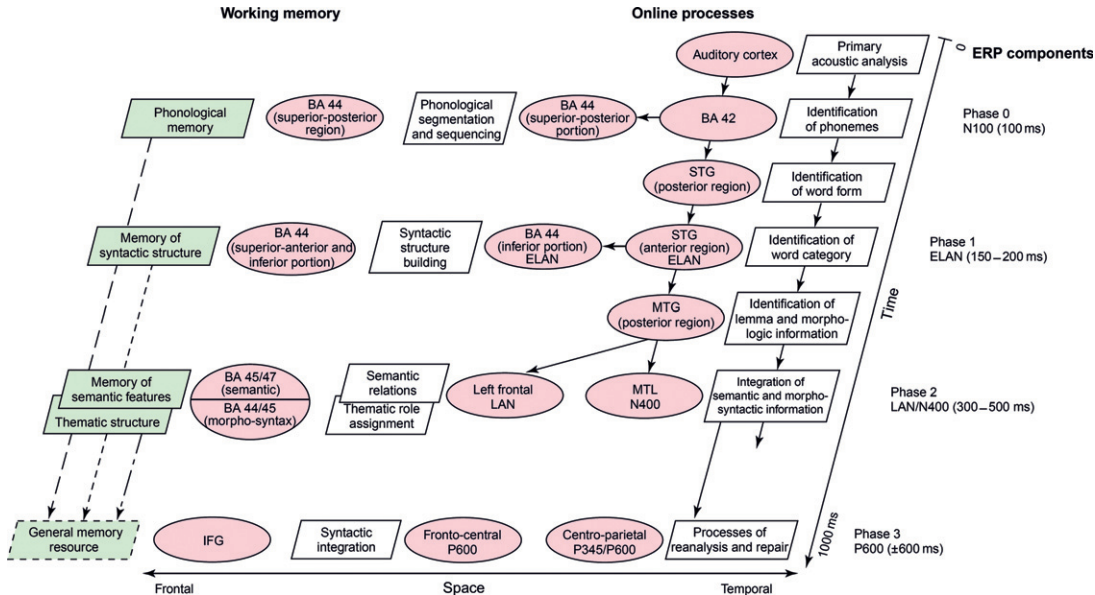


FIGURE 11.11 Putting it all together. A model of auditory sentence processing. The boxes represent the functional processes; in parentheses we see neural correlates identified by brain imaging. Abbreviations: BA, Brodmann's area; ELAN, early leftanterior negativity; ERP, event-related brain potential; fMRI, functional magnetic resonance imaging; IFG, inferior frontal gyrus; MTG, middle temporal gyrus; MTL, middle temporal lobe; PET, positron imaging tomography; STG, superior temporal gyrus. Source: Friederici, 2002.

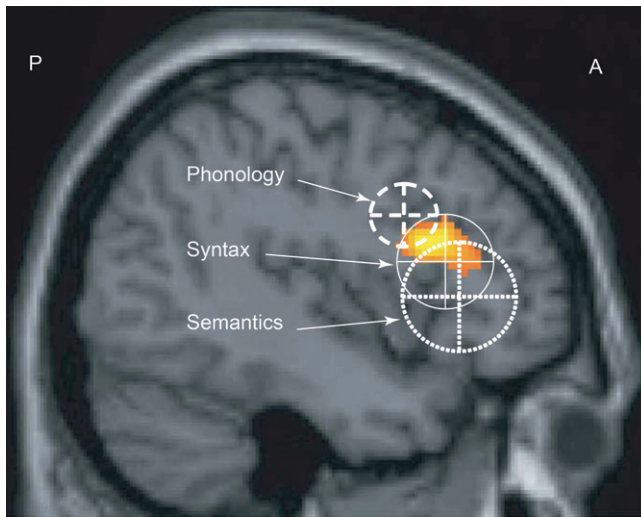


FIGURE 11.12 An area of integration? Hagoort (2005) points out that Broca's area has multiple functions that go beyond the control of speech. He suggests that an expanded version of Broca's area may be a zone of unification for speech and meaning. This expanded region is called the left inferior frontal gyrus (left, lower, frontal fold of the cortex, or LIFG). Source: Hagoort, 2005, Figure 5.

the evoked potential (Friederici, 2002). For example, semantic information is known to trigger a large negative wave 400 ms after a stimulus (called N400).

If this seems awesomely complex, that seems to be the reality of our language abilities. The kind of complexity we see in Figure 11.11 evolved over many generations. The biological readiness of our brains for this complex activity has many evolutionary layers, some shared with other mammals and other species. Our vocabulary is much more recent, of course, and we can even watch the changes in vocabulary that happen over a few years.

The visual system seems to have a region of integration "where everything comes together," perhaps in the inferotemporal cortex (area IT) (Sheinberg & Logothetis, 1997). In that patch of cortex, neurons respond not to single retinal stimuli and not even to separate features like colors or light edges. Area IT picks up entire visual objects, and neighboring regions seem to respond to visual scenes. Language may have a similar region of integration, where many levels of control and representation come together (Figure 11.12) (Hagoort, 2005).

9.0 SUMMARY

Language is a distinctive human capacity, one that makes it possible to transmit cultural knowledge and skills over space and time. Broca's area for speaking and Wernicke's for speech comprehension are only part of the large cortical regions involved. Current work has expanded and fractionated the traditional language areas, so the left inferior frontal gyrus (LIFG) is a better term than Broca's area. The auditory and speech perception regions of the parietal and temporal cortex are better terms than "Wernicke's area." There is constant interplay between motor and sensory language areas. The right hemisphere has its own role to play in language perception.

Each level of linguistic description now has neuroimaging evidence (see Figure 11.1). So much of speech and language is dependent on long-term memory, however, that many scientists believe that we must ultimately look for widely distributed cortical networks to explain our vocabulary, syntax, and semantics. These networks depend on the synaptic connectivities of very large numbers of neurons. We are just beginning to understand such weblike patterns of distributed neurons.

10.0 STUDY QUESTIONS AND DRAWING EXERCISES

1. Fill in the labels in [Figure 11.13](#) of processing hierarchies of language.
2. Give examples of the need for 'top-down' or 'expectation-driven' processing in the input flow of speech. What about the output flow?
3. In what respects does the human vocal apparatus resemble a musical instrument?

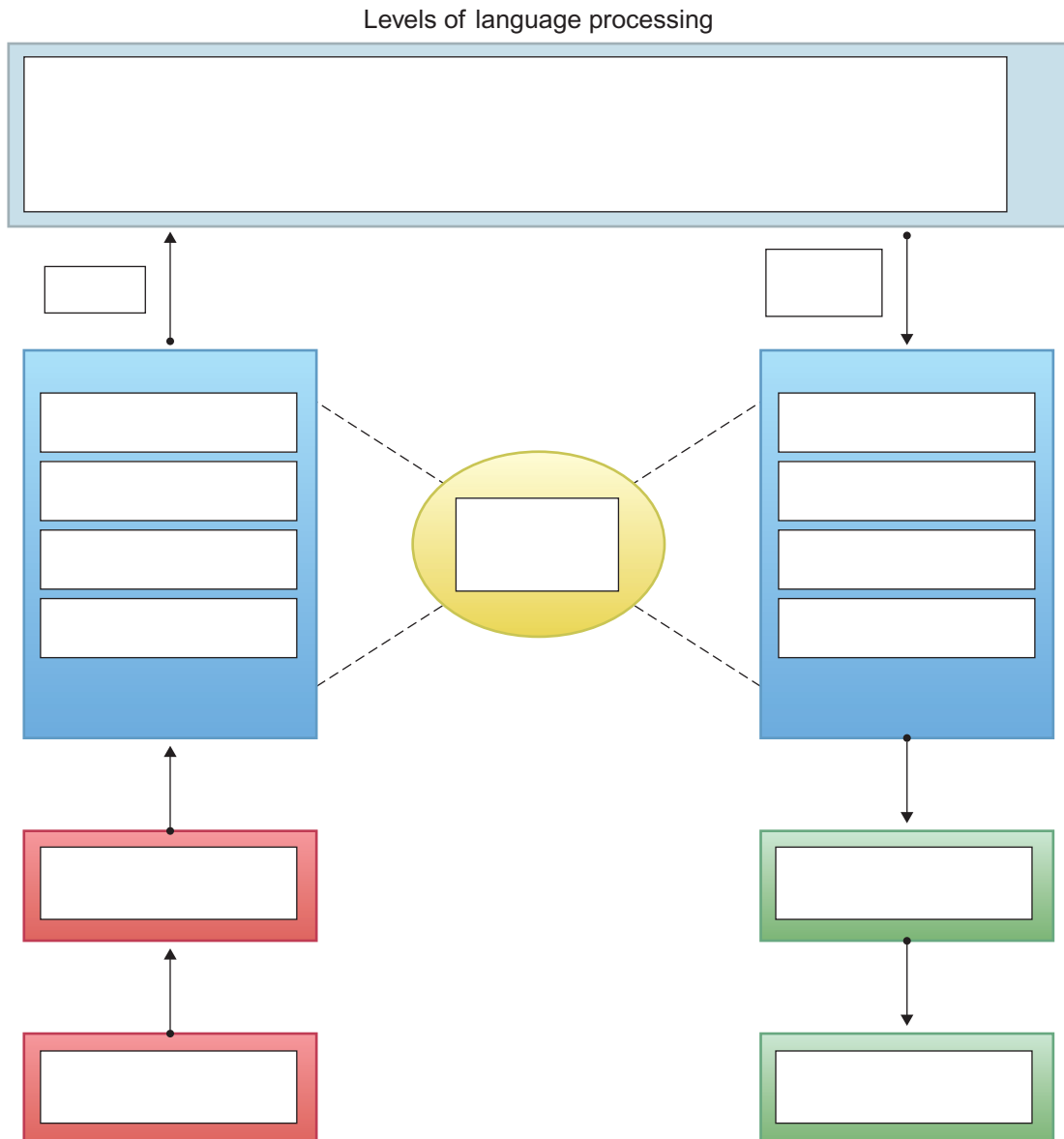


FIGURE 11.13 Linguistic processing hierarchy. Complete the text inside the boxes based on what you learned in this chapter.

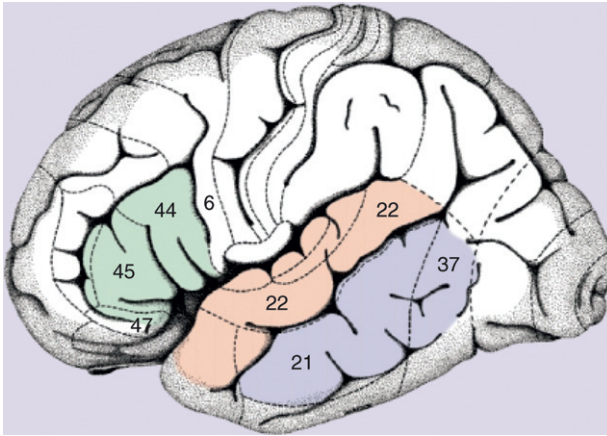


FIGURE 11.14 Based on what you have read and learned in this chapter, can you make an educated guess about the language function of the shaded brain regions? Note—you may want to consult other chapters in the text to confirm your ideas.

4. In [Figure 11.14](#), show the following:
 - a. A cortical region likely to be involved in speech preparation
 - b. One for speech planning
 - c. One for motor control of the vocal tract, such as the tongue
5. What is the approximate size of the lexicon (vocabulary of natural language)?

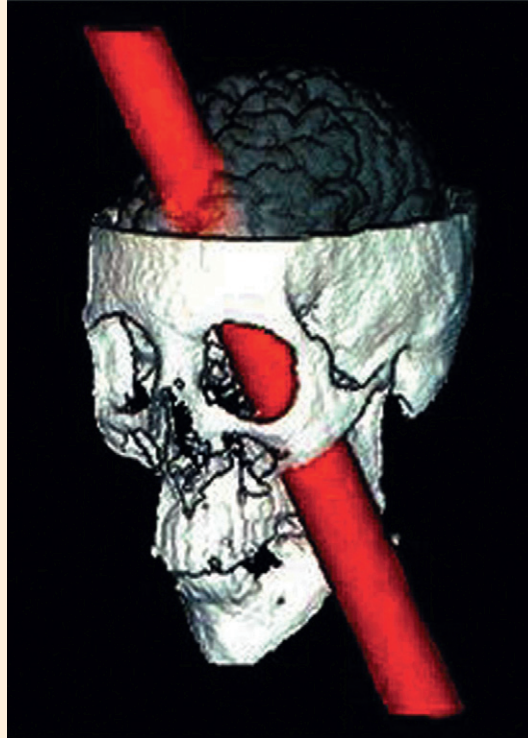
Decisions, goals, and actions

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A RECONSTRUCTION OF THE INJURY TO PHINEAS GAGE

He is fitful, irreverent, indulging at times in the grossest profanity (which was not previously his custom), manifesting but little deference for his fellows, impatient of restraint or advice when it conflicts with his desires. . . . A child in his intellectual capacity and manifestations, he has the animal passions of a strong man. . . . His mind was radically changed, so decidedly that his friends and acquaintances said he was "no longer Gage." *John Martyn Harlow*



A reconstruction of Phineas Gage's railroad accident in 1848, when he was 25 years old. Notice likely damage to the orbitofrontal and medial frontal regions as well. Injuries like this create damage from swellings, bleeding, heat, infection, inflammation, and physical twisting of tissues that extend far beyond the immediate region of impact. Thus we do not really know the extent of brain damage in this classic neurological patient.

Source: *Squire et al., 2008.*

1.0 INTRODUCTION

What do these behaviors have in common? Remembering your friend's new cell phone number while looking for a piece of paper. Deciding to study first and play basketball second. Planning a new route when a road has been closed for repair. Paying attention while you are

reading this sentence. Changing your mind about raising the stakes in a poker game. All of these behaviors—and many more—are guided by the frontal lobes.

1.1 The many and complex frontal lobe functions

The frontal lobes have been described as a control center for functions such as paying attention selectively to one item rather than another, making plans and revising them when needed, monitoring the world around us—complex functions that are part of our everyday life. The frontal lobes also are described as the “action lobes” where physical actions are planned and motor system activity is initiated. The frontal lobes also are described as the “home” of our personality and social morality. How does one brain region provide these diverse and complex functions?

The answer to this question is still being investigated, but we have learned about frontal lobe function through many investigative pathways. In animal research, we have learned about the role of the frontal lobe using single unit recordings. In humans, we have learned about the many roles of the frontal lobe through brain damage and disease. A key figure in our knowledge about frontal lobe function is Phineas Gage, the railroad worker who had major frontal lobe damage due to a railroad accident. Phineas’s sudden personality change following the accident shed light on the role of frontal regions in personality formation and in social cognition. Studies of people who have had frontal lobe damage through disease, brain injury, or disorder have aided us in developing categories of frontal lobe function based on where the brain damage or disease has occurred and the resultant change in behavior. More recently, neuroimaging studies of healthy individuals have provided new information about the localization of patterns of frontal lobe activity occurring during tasks that tap frontal lobe functions, such as voluntary or executive attention and decision making.

The frontal lobes are a vast mosaic of cell types and cortical regions, diverse in their cell structures, anatomical features, and connectivity patterns. Unlike regions in sensory cortex, the frontal lobes do not have a single job to do; they are not specialized for decoding speech sounds or recognizing faces. Rather, the frontal lobes are engaged in almost all aspects of human cognitive function.

In this chapter, we present the results of neuroimaging studies that have provided new data on where, what, and how specific regions in the frontal lobes are activated during cognitive tasks. Next, we look at frontal lobe syndromes that are observed in patients with damage to the frontal lobe and connected regions. Finally, we examine how the results of neuroimaging and patient studies combine to inform us about the role of the frontal lobes in human behavior.

1.2 From the silent lobes to the organ of civilization

It took scientists many years to begin to appreciate the importance of the frontal lobes for cognition. But when this finally happened, a picture of particular complexity and elegance emerged. The frontal lobes used to be known as “the silent lobes” because they are not easily linked to any single, easily defined function. Now it is known that the frontal lobes play a key role in almost every aspect of human behavior, including decision making, social and

personality behaviors, and planning strategies. The frontal lobes are not silent after all; they are the organ of civilization!

If the frontal lobes are the “organ of civilization,” then what exactly is their function? What is their “civilizing” effect? The functions of the frontal lobes defy a simple definition. They are not invested with any single, ready-to-label function. A patient with frontal lobe damage will typically retain the ability to move around, use language, recognize objects, and even memorize information.

For the most part, this chapter focuses on the prefrontal cortex (PFC), the most anterior part of the frontal lobes, in front of the motor areas. There are many subregions in the PFC, but four regions most typically are identified when assessing their functional role in cognition: *dorsolateral PFC* (DLPFC), *ventrolateral PFC* (VLPFC), *anterior PFC* (APFC), and *medial PFC* (MPFC) (Figure 12.1). PFC is located in front of the primary motor cortex, sometimes called the motor strip.

PFC plays the central role in forming goals and objectives and then in devising plans of action required to attain those goals. It selects the cognitive skills needed to implement the plans, coordinates these skills, and applies them in a correct order. Finally, the PFC is responsible for evaluating our actions as success or failure relative to our intentions. See Table 12.1 for other common prefrontal functions.

1.3 “Memory of the future”

David Ingvar (1985) coined the phrase “memory of the future.” Ingvar was referring to one of the most important functions of advanced organisms: making plans and then following the plans to guide behavior. Unlike primitive organisms, humans are active, rather than reactive,

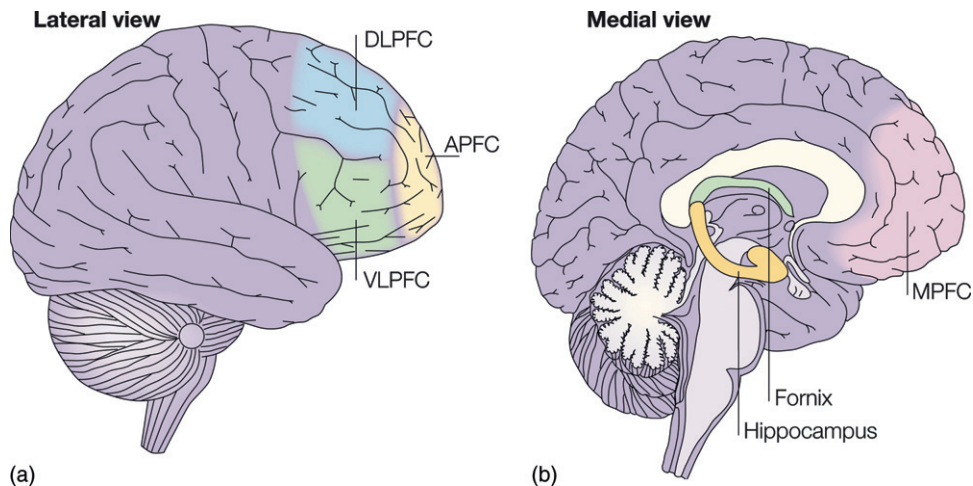


FIGURE 12.1 The major divisions of the prefrontal cortex. The prefrontal cortex can be divided into lateral (side), medial (midline), ventral (bottom), and frontal regions. The lateral division divides into upper (dorsal) and lower (ventral) halves, separated by a major horizontal fold, the inferior lateral sulcus. Source: *Simons and Spiers, 2003*.

TABLE 12.1 Some Common Prefrontal Functions

1. Planning, setting goals, and initiating action
2. Monitoring outcomes and adapting to errors
3. Mental effort in pursuing difficult goals
4. Interacting with other regions in pursuit of goals (basal ganglia, thalamic nuclei, cerebellum, motor cortex)
5. Having motivation, being willing to engage in action
6. Initiating speech and visual imagery
7. Recognizing other people's goals, engaging in social cooperation and competition
8. Regulating emotional impulses
9. Feeling emotions
10. Storing and updating working memory
11. Active thinking
12. Enabling conscious experiences
13. Sustained attention in the face of distraction
14. Decision making, switching attention, and changing strategies
15. Planning and sequencing actions
16. Unifying the sound, syntax, and meaning of language
17. Resolving competition between plans

beings. The transition from mostly reactive to mostly proactive behavior is among the central themes of the evolution of the nervous system. We are able to form goals, our visions of the future. Then we act according to our goals. But in order to guide our behavior in a sustained fashion, these mental images of the future must become the content of our memory; thus the “memories of the future” are formed.

Human cognition is forward-looking, *proactive* rather than *reactive*. It is driven by goals, plans, hopes, ambitions, and dreams, all of which pertain to the future and not to the past. These cognitive powers depend on the frontal lobes and evolve with them. The frontal lobes endow the organism with the ability to create neural models as a prerequisite for making things happen, models of something that, as of yet, does not exist but that you *want* to bring into existence.

To make plans for the future, the brain must have an ability to take certain elements of prior experiences and reconfigure them in a way that does not copy any actual past experience or present reality exactly. To accomplish that, the organism must go beyond the mere ability to *form* internal representations, the models of the world outside. It must acquire the ability to *manipulate and transform* these models. We can argue that tool making, one of the fundamental distinguishing features of primate cognition, depends on this ability, since a tool does not exist in a ready-made form in the natural environment and has to be *imagined* in order to be made. The neural machinery for creating and holding “images of the future” was a *necessary prerequisite* for tool making and thus for launching human civilization.

We can also argue that the generative power of language to create new ideas depends on this ability as well. The ability to manipulate and recombine internal representations depends critically on the PFC, which probably made it critical for the development of language.

1.4 Self-awareness and executive function

Goal formation is about “I need” and not about “it is.” Therefore, the ability to formulate goals must have been inexorably linked to the emergence of the mental representation of self. It should come as no surprise that *self-awareness* is also intricately linked to the frontal lobes. All these functions can be thought of as metacognitive rather than cognitive, since they do not refer to any particular mental skill but provide an overarching organization for all of them. For this reason, some authors refer to the functions of the frontal lobes as *executive functions*, by analogy with a governmental or corporate executive.

1.5 Frontal lobe development

If it seems to you that the role the frontal lobes play in cognition seems uniquely human, you are right! The vast expansion of the frontal lobes during evolution and their maturational path during the lifetime in humans are unique among living creatures.

In evolution, the frontal lobes accelerated in size only with the great apes. These regions of cortex underwent an explosive expansion at the late stage of evolution. According to Brodmann (1909), the PFC or its analogs account for 29 percent of the total cortex in humans, 17 percent in the chimpanzee, 11.5 percent in the gibbon and the macaque, 8.5 percent in the lemur, 7 percent in the dog, and 3.5 percent in the cat (Figure 12.2). While whales and dolphins have large brains, it is the *parietal* rather than the frontal cortex that has expanded in these aquatic mammals.

As the seat of goals, foresight, and planning, the frontal lobes are perhaps the most uniquely human of all the components of the human brain. In 1928, the neurologist Tilney suggested that all human evolution should be considered the “age of the frontal lobe,” but scientific interest in the PFC was late in coming. Only gradually did it begin to reveal its secrets to the great scientists and clinicians like Hughlings Jackson (1884) and Alexander Luria (1966), and in the last few decades to researchers like Antonio Damasio (1995), Joaquin Fuster (1997), Patricia Goldman-Rakic (1987), Donald Stuss and Frank Benson (1986), and others.

2.0 STRUCTURE OF THE FRONTAL LOBES

As we have mentioned before, the neuroanatomy and neurophysiology of the frontal lobes reflect their diverse and complex functions, with many distinct regions that differ sharply in their cellular and anatomical structure. Adding another layer of complexity is their high degree of connectivity across many brain regions. In this section, we highlight the main subdivisions of the frontal lobes and show the amazing neural highways that connect them to the rest of the brain.

2.1 Neuroanatomy and neurophysiology of the frontal lobes

The boundaries of the frontal lobes typically are described using gross anatomical structures and Brodmann areas to define boundaries of frontal lobe regions. A simple way to think of the location of the frontal lobes is that they lie *in front of* the central sulcus that separates them from the parietal lobes and *above* the Sylvian fissure that separates them from the temporal lobes (see Figure 2.1).

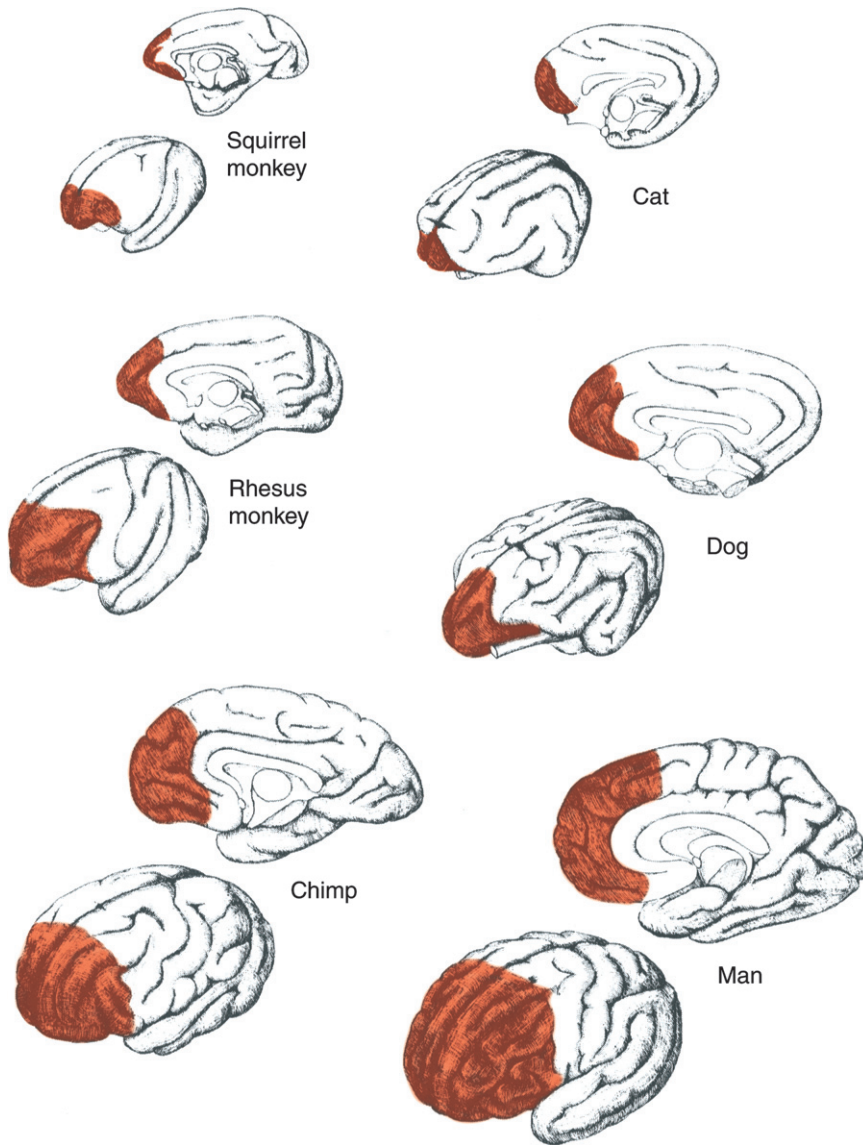


FIGURE 12.2 The prefrontal cortex expands over mammalian and primate evolution. A greatly enlarged prefrontal cortex is a distinctively human and primate feature. Other large-brained mammals like whales and dolphins have expanded parietal rather than prefrontal regions. Bottom right, a human brain, with a chimp brain on the bottom left. Source: *Squire et al., 2003*.

2.2 How prefrontal cortex is defined

A more precise definition of PFC can be accomplished by using *Brodmann area* maps (Brodmann, 1909). Brodmann areas are based on the types of neurons and connections that typically are found there within. According to this definition, the PFC consists of Brodmann

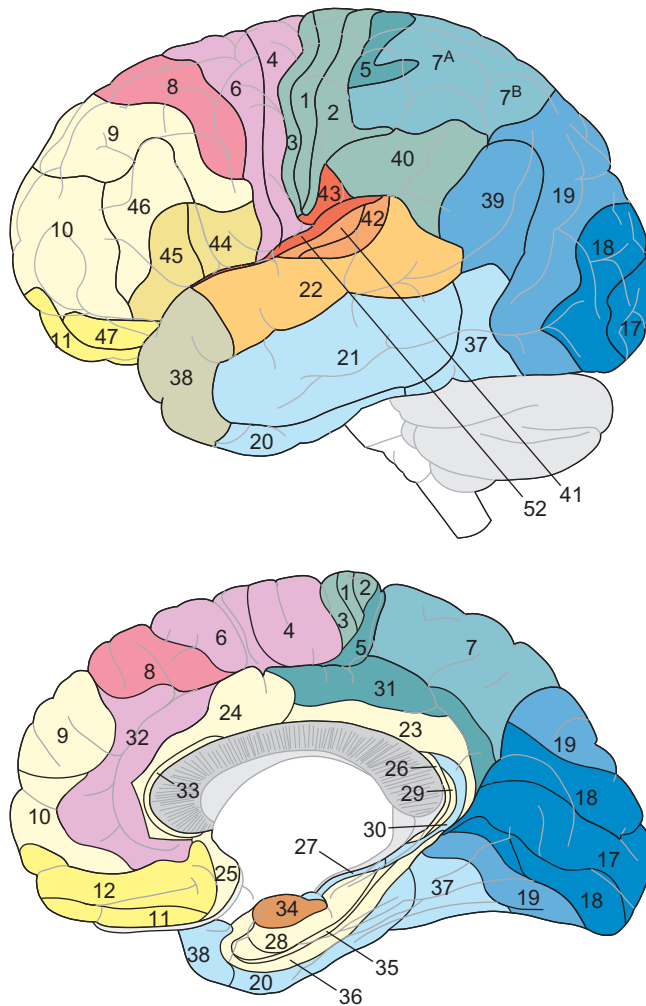


FIGURE 12.3 Brodmann areas in the frontal lobes. Areas forward of the motor cortex are considered to be prefrontal. (Brodmann areas 4 and 6 are motor and premotor regions.) However, the boundary is not rigid. It is often useful to think of a gradual transition between more “cognitive” areas and primary motor cortex (BA 4), which directly controls voluntary muscles. Source: Adapted by Bernard J. Baars from M. Dubin, with permission; drawn by Shawn Fu.

areas 8, 9, 10, 11, 12, 13, 44, 45, 46, and 47 (Figure 12.3) (Fuster, 1997). These areas are characterized by the predominance of the so-called granular neural cells found mostly in layer IV (Campbell, 1905, in Fuster, 1997).

Another method of outlining the PFC is through its subcortical projections. Fuster (2008) has hypothesized a perception-action cycle including PFC and posterior regions of the brain and subcortical nuclei including the thalamus (Figure 12.4). Note that PFC has *bidirectional* connections between many subcortical regions.

Finally, the PFC sometimes is delineated through its biochemical pathways. According to that definition, the PFC is defined as the area receiving projections from the mesocortical dopamine system. These various methods of delineating the PFC outline roughly similar territories.

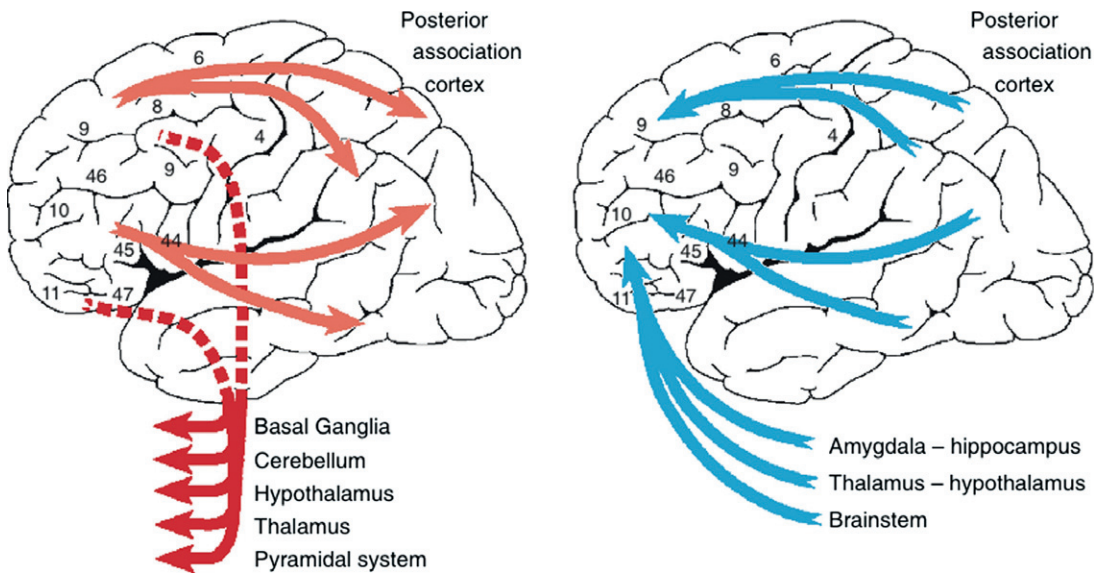


FIGURE 12.4 A schematic diagram of connections *from* (shown in red) the prefrontal cortex to posterior brain regions and to subcortical nuclei. Connections to the prefrontal cortex are shown in blue. Source: Fuster, 2008.

2.3 The vast connective highways of the frontal lobes

The PFC is connected directly with every distinct functional unit of the brain (Nauta, 1972). It is connected to the highest levels of perceptual integration, and also with the *premotor cortex*, *basal ganglia*, and the *cerebellum*, all involved in aspects of motor control and movements. PFC also is connected with the *dorsomedial thalamic nucleus*, often considered to be the highest level of integration within the thalamus; with the *hippocampi* and *medial temporal structures*, known to be critical for memory; and with the *cingulate cortex*, believed to be critical for emotion and dealing with uncertainty. In addition, PFC connects with the *amygdala*, which regulates most emotions and social cognition, and with the *hypothalamus*, which is in charge of control over the vital homeostatic functions of the body. Finally, PFC is also well connected with the *brain-stem* nuclei involved in wakefulness, arousal, and overall alertness, regulation of sleep and REM dreams.

This unique connectivity makes the frontal lobes singularly suited for coordinating and integrating the work of other brain structures (Figure 12.5). This extreme connectivity also puts the frontal lobes at a particular risk for disease. Some scientists believe that the PFC contains a map of the whole cortex, an assertion first made by Hughlings Jackson (1884) at the end of the nineteenth century. This hypothesis asserts that prefrontal regions are needed for normal consciousness. Since any aspect of our mental world may, in principle, be the focus of our consciousness, it stands to reason that an area of convergence of all its neural substrates must exist. This leads to the provocative proposition that the evolution of consciousness, the highest expression of the developed brain, parallels the evolution of the PFC.

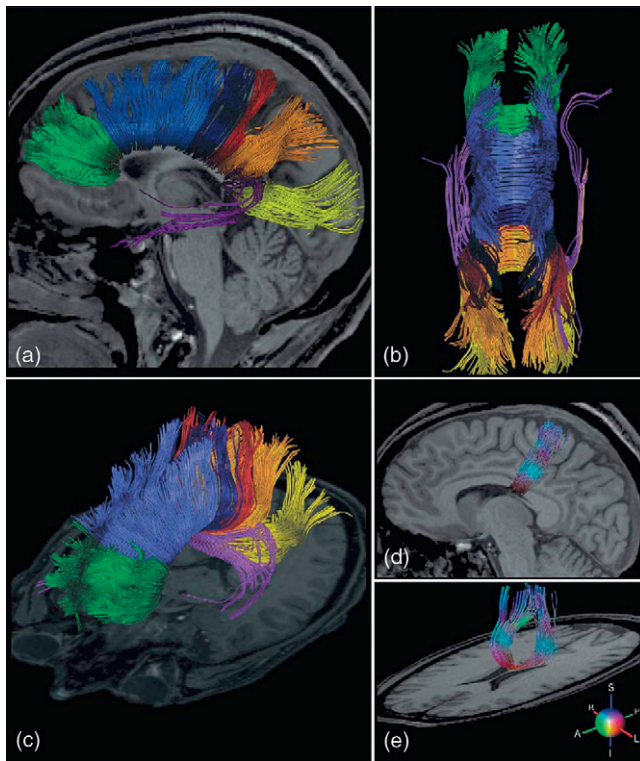


FIGURE 12.5 Fiber bundles in the brain are shown in midsagittal, horizontal, and coronal sections. See the Brain Atlas, Plate 2 for reference. (a) Centerline of the brain (midsagittal) view of the fiber bundles extending into the prefrontal cortex, shown in green, and into the premotor and motor cortex, shown in blue. (b) A horizontal slice (axial view) of the same fiber bundles. (c) A coronal slice showing the same green and blue fibers at the front of the brain. (d) and (e) show sagittal (d) and oblique (e) views of callosal fiber tracts that project into primary motor cortex. The color coding reflects the diffusion direction as indicated in the lower right corner, with A = anterior, I = inferior, L = left, P = posterior, R = right, S = superior. Source: Hofer & Frahm, 2006.

3.0 A CLOSER LOOK AT FRONTAL LOBE FUNCTIONS

3.1 Executive functions

The concept of executive functions is inextricably linked to the function of the frontal lobes. The groundwork for defining the executive functions system was laid by Alexander Luria (1966) as early as 1966. At the time, Luria proposed the existence of a system in charge of intentionality, the formulation of goals, the plans of action subordinate to the goals, the identification of goal-appropriate cognitive routines, the sequential access to these routines, the temporally ordered transition from one routine to another, and the editorial evaluation of the outcome of our actions.

Subsequently, two broad types of cognitive operations linked to the executive system figured most prominently in the literature:

1. One's ability to guide one's behavior by the formulation of plans, and then guiding behavior according to these plans
2. One's ability not only to guide one's behavior but having the capacity to "switch gears" when something unexpected happens

To deal effectively with such transitions, a particular ability is needed—*mental flexibility*—which is the capacity to respond rapidly to unanticipated environmental contingencies. Sometimes this is referred to as an ability to shift *cognitive set*. Additionally, the executive system is critical for planning and the generative processes (Goldberg, 2001a).

Fuster (1997) enlarged on the premise originally developed by Luria by suggesting that the so-called executive systems can be considered functionally homogeneous in the sense that they are in charge of actions, both external and internal (such as logical reasoning). In general, the executive functions are not unique to humans. However, the uniqueness of the human executive functions is in the *extent* to which they are capable of integrating such factors as time, informational novelty, and complexity, and possibly ambiguity.

3.2 Social maturity and moral development

While many neuroimaging and behavioral studies have investigated attention, working memory, and executive control processes in the PFC, the frontal lobes also play a critical role in the development of social cognition—a key link to the role of the frontal lobes as the “organ of civilization.” The capacity for volitional control over one’s actions is not innate, but it emerges gradually through development and is an important, perhaps central, ingredient of *social maturity*.

3.2.1 Early life experience and orbitofrontal cortex development

Parent-infant interactions during the first months of life are thought to be key to the normal development of the orbitofrontal cortex (Figures 12.6 and 12.7) (Schoore, 1999). By contrast, early-life stressful experiences permanently damage the orbitofrontal cortex, predisposing the individual to later-life psychiatric diseases. This implies that early social interactions help shape the brain. One critical element in this learning is eye gaze. When the infant and parent have mutual eye gaze, they establish the neural underpinnings of understanding another’s intentionality and empathy that are key to social development (see Chapters 13 and 14).

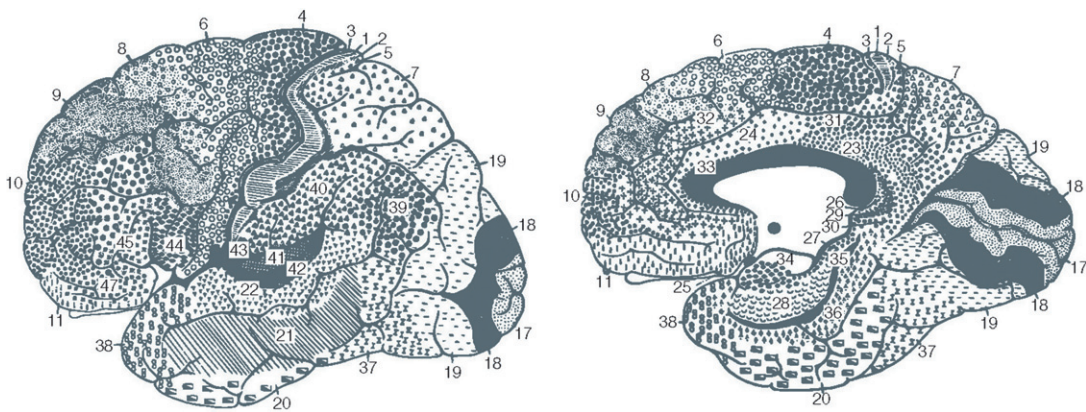


FIGURE 12.6 Cytoarchitectonic maps of the brain—areas 10, 11, and 47 comprise the orbitofrontal cortex. Source: Kringsbach, 2005.

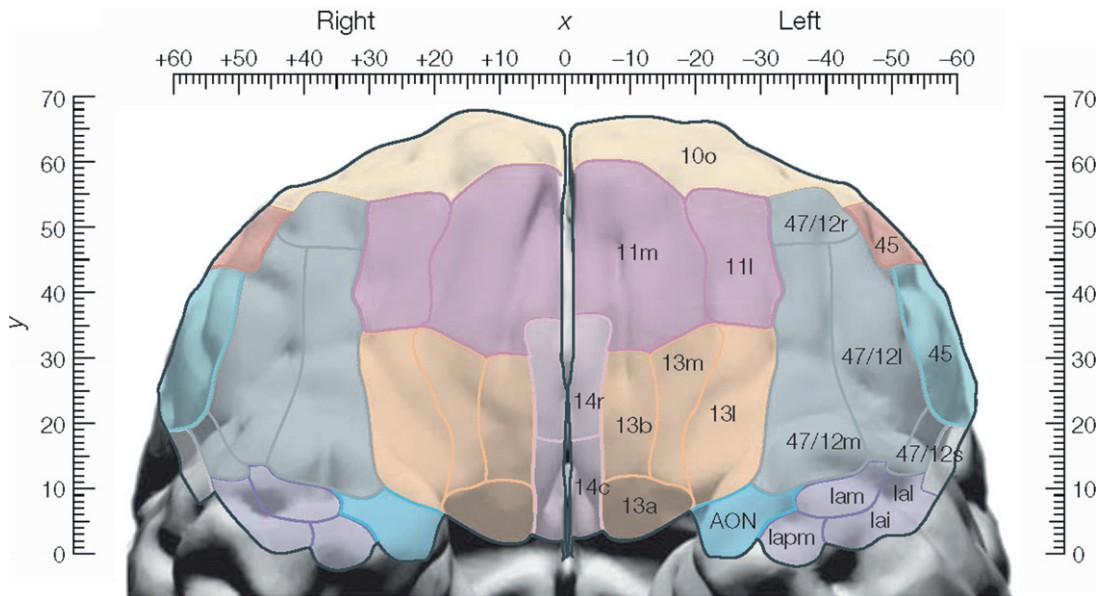


FIGURE 12.7 Another view of the orbitofrontal cortex looking from the front of the brain. Source: Kringsbach, 2005.

The orbitofrontal cortex is perhaps the least well-understood region in the prefrontal cortex. Recent neuroimaging advances are providing new data for understanding this region's role in human behavior and cognition, but its role is still being elucidated. A current view of the role of the orbitofrontal cortex in adults is that it plays a key role in emotional and reward related behaviors such as making predictions, risk assessment, and decision making (Kringsbach, 2005). These emotional and reward-related behaviors are frequently associated with aspects of human behavior that involve risk, such as gambling, illegal drug use, and thrill-seeking activities. According to our current knowledge, the orbitofrontal cortex is a very slow-to-mature region of the brain, with maturation continuing throughout adolescence (Figure 12.8). The late-to-mature aspect of the orbitofrontal cortex may be associated with risk-taking behaviors observed during the teenage years (Galvan et al., 2006).

3.2.2 Moral development and the frontal cortex

Furthermore, following this logic, is it possible that moral development involves the frontal cortex, just as visual development involves occipital cortex and language development involves temporal cortex? The PFC is the association cortex of the frontal lobes, the "action lobes." The posterior association cortex encodes generic information about the outside world. It contains the taxonomy of the various things known to exist and helps recognize a particular exemplar as a member of a known category. By analogy, the PFC may contain the taxonomy of all the *sanctioned moral actions and behaviors*. And could it be that, just as damage or maldevelopment of the posterior association cortex produces *object agnosias*, so does damage or maldevelopment of the PFC produce, in some sense, *moral agnosia*?

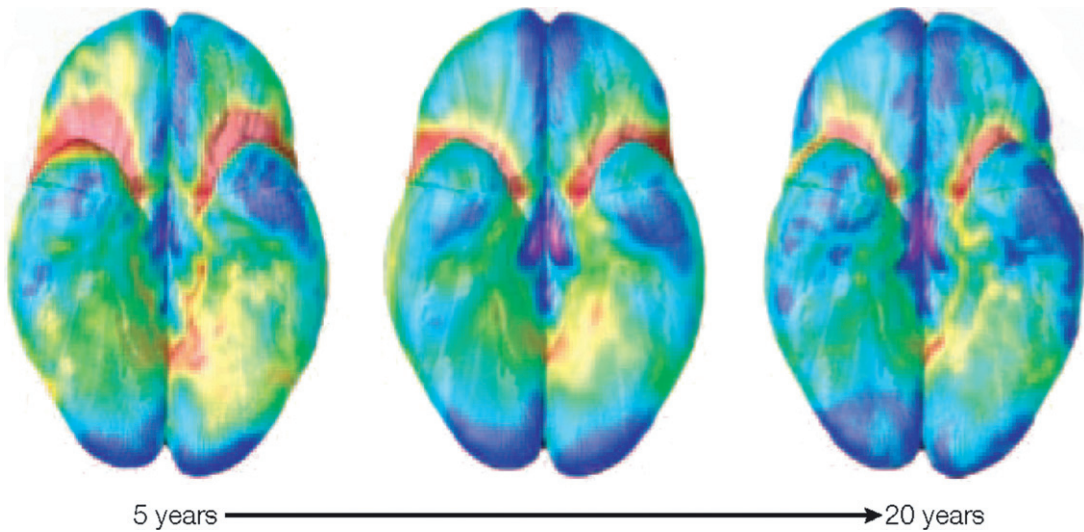


FIGURE 12.8 A bottom view of the brain showing the changes in cortical gray matter from young children (5 years, left brain figure) as compared to young adults (20 years, right brain figure). The color shows gray matter volume from low (blue) to high (pink). The orbitofrontal cortex is later to mature than neighboring regions. Source: Gogtay *et al.*, 2004.

A report by Damasio and colleagues lends some support to this idea (Anderson *et al.*, 1999). Damasio studied two young adults, a man and a woman, who suffered damage to the frontal lobes very early in life. Both engaged in antisocial behaviors: lying, petty thievery, truancy. Damasio claims that not only did these patients fail to act according to the proper, socially sanctioned moral precepts, but they even failed to recognize them as morally wrong.

The orbitofrontal cortex is not the only part of the frontal lobes linked to socially mature behavior. The *anterior cingulate cortex* occupies a midfrontal position and is closely linked to the PFC. The anterior cingulate cortex traditionally has been linked to emotion. According to Michael Posner, it also plays a role in social development by regulating distress (Posner & Rothbart, 1998).

3.2.3 Age of maturity and frontal lobe development

The implicit definition of social maturity changes throughout the history of society, and so does the time of “coming of age.” In modern Western societies, the age of 18 (or thereabouts) has been codified in the law as the age of social maturity. This is the age when a person can vote and is held responsible for his or her actions as an adult. The age of 18 is also the age when the maturation of the frontal lobes is relatively complete. Various estimates can be used to measure the course of maturation of various brain structures. Among the most commonly used such measures is pathway myelination (Yakolev & Lecours, 1967). The frontal lobes cannot fully assume this role until the pathways connecting the frontal lobes with the far-flung structures of the brain are fully myelinated.

The agreement between the age of relatively complete maturation of the frontal lobes and the age of social maturity is probably more than coincidental. Without the explicit benefit of

neuroscience, but through cumulative everyday common sense, society recognizes that an individual assumes adequate control over his or her impulses, drives, and desires only by a certain age. Until that age, an individual cannot be held fully responsible for his or her actions in either a legal or moral sense. This ability appears to depend critically on the maturity and functional integrity of the frontal lobes.

4.0 NEUROIMAGING THE EXECUTIVE BRAIN

The two broad types of cognitive operations linked to the executive systems in the frontal lobe have been extensively investigated using functional neuroimaging techniques such as PET and fMRI. We summarize some general findings here, separating the results into three sections: *attention and perception*, *working memory*, and *executive function and motor control*. But first a word of caution about functional neuroimaging studies of complex processes: As we have described, the PFC is intricately involved in many cognitive and executive processes such as paying attention, holding something in mind for a few moments, switching attention when needed, and making decisions. Thus *any task* used in a neuroimaging study will necessarily involve these complex and overlapping processes in the frontal lobe and elsewhere in the brain. In fact, just participating in the study engages the subject—and their frontal lobes—in complicated ways (for a good discussion of these issues, see Fuster, 2008).

In order to disentangle the many processes engaged in any task, investigators studying frontal lobe function need to carefully design their studies so they can identify which processes are specifically related to, for example, attention versus working memory, which are aspects of almost any task. In the following section, we present a brief summary of many neuroimaging studies that have looked at these prefrontal processes.

4.1 Attention and perception

Imagine that you are a subject in an fMRI study. Your task is to look at a screen, and when you see a picture of a male face, you are to press one button, and if you see a picture of a female face, you press another button. Easy, right? What parts of the brain will be activated by this task? You might suggest that the visual cortex will be busy, based on your knowledge of sensory activity in the brain. You might also suggest that the fusiform face area (see [Chapter 6](#)) will “light up” for this task. And you would be correct. But there are other aspects of this task that will activate the brain: paying attention to the screen, making a decision about whether the face is male or female, preparing to press a button, and then actually pressing the button—all key aspects of frontal lobe function. In fact, this is a central finding in neuroimaging studies of visual or auditory perception; many areas in the brain outside of sensory cortex are activated.

But first a word about attention. In this chapter about frontal lobe functions, we will be discussing *voluntary attention*. This is the aspect of attention in which we are in control of what we decide to pay attention to. When reading this sentence, for example, you are deciding to focus on the words and their meaning and not on the font type or size, or the sound of the clock ticking at your elbow. Voluntary attention often is called *executive attention* or *top-down*

attention to indicate that it is the class of attentional processes that are under our control. Another type of attention is involuntary; these are automatic, frequently stimulus-induced processes whereby our attention is “grabbed” by something in our environment. For example, the ringing of your cell phone, the sudden bright light when the sun comes from behind a cloud, the aroma of coffee brewing all may temporarily attract your attention without any conscious effort on your part. Automatic attentional processes can serve to disrupt our voluntary attention, but both are critical for being able to plan and initiate behavior—whether that behavior is finishing an essay for class in the morning or jumping out of the way when a car horn sounds behind you. The push and pull of voluntary and involuntary attentional processes are key functions of the frontal lobes.

An early investigation used PET to show localization patterns for sustained voluntary attention and provided important new information about prefrontal regions that subserved voluntary attentional processes (Pardo et al., 1991). At about the same time, seminal work on the voluntary attentional networks involved in perceptual tasks was provided by Michael Posner and Steve Petersen (Posner & Petersen, 1990), where they detailed an anterior attentional system, which they described as having three major separable networks that perform the alerting, orienting, and executive (conflict resolution) voluntary attentional functions that are important to many tasks. Over the years, Posner and his colleagues developed an attention network test (ANT) that provided them with ways to separately measure and record brain regions that subserve these voluntary attentional networks. The anterior attentional system they describe has three key networks: *alerting*, for maintaining an alert state, such as being ready to look at visual images in the previous scanner example; *orienting*, such as preparing to see a new visual image of a face that appears in the scanner; and *executive*, such as deciding whether the face is male or female.

These networks are shown visually in the brain in Figures 12.9, 12.10, and 12.11. Figure 12.9 details fronto-parietal regions that are part of the alerting network, Figure 12.10 shows parietal lobe regions that are active in the orienting network, and Figure 12.11 shows frontal and many other regions that are active in the executive or conflict resolution network.

Another central finding from these and other studies of anterior voluntary attention networks is that the *level of activity* in the PFC corresponds to the *level of attention* required by the task, with more activity for tasks with higher attentional demands (Posner et al., 1988; Pardo et al., 1990). A part of the prefrontal region that typically is activated by tasks requiring focused attention is the anterior cingulate gyrus in the anterior cingulate cortex (ACC) (Posner et al., 1988; Raichle, 1994).

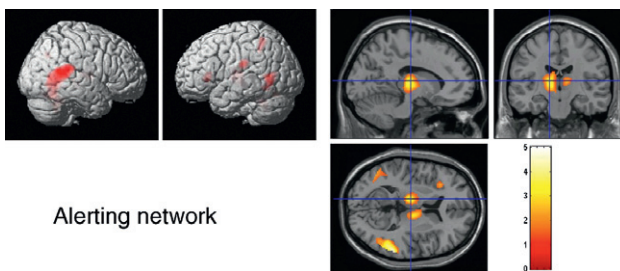


FIGURE 12.9 fMRI results for the alerting attentional network. The cross-section view of activations shows the thalamic activations of the alerting effect. Source: Fan et al., 2005.

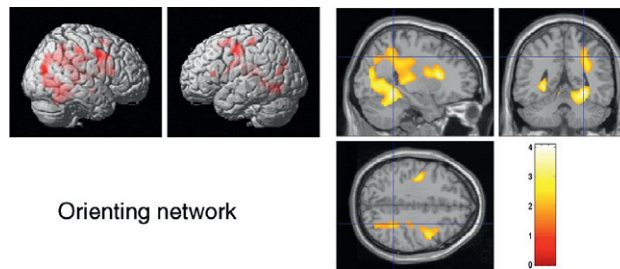


FIGURE 12.10 fMRI results for the orienting attentional network. The cross-section view of activations shows parietal activation. Source: Fan *et al.*, 2005.

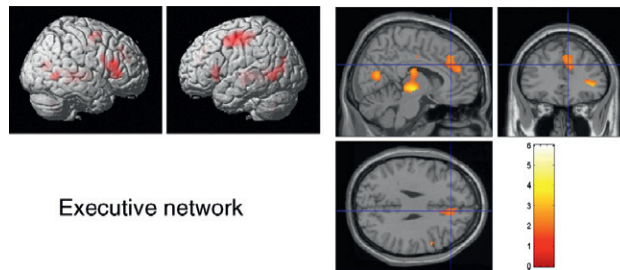


FIGURE 12.11 fMRI results for the conflict attentional network. The cross-section view of activations shows ACC activation. Source: Fan *et al.*, 2005.

4.2 Working memory

The ability to keep something in mind for a limited amount of time is a central function in cognition. This ability—working memory—is closely associated with voluntary attentional systems. In fact, one way of describing working memory is that it serves as an *inward directed voluntary attention* system, directing attention to internal representations (Fuster, 2008). A central issue in investigating brain areas that subserve working memory is, how do you study working memory and separate findings from other executive processes such as attention and decision making? To accomplish this, D'Esposito and colleagues (1995) developed a dual task paradigm using two tasks that, individually, did not have working memory demands. Together, however, they did produce working memory demands, and in this way, D'Esposito and colleagues were able to isolate processes that were specific to working memory function and not to general task performance. They identified regions in the PFC that were specifically involved in working memory processes, providing important new data on separable aspects of central executive functions in PFC.

In his book, *The Prefrontal Cortex*, Fuster (2008) presents a meta-analysis of several neuroimaging studies of working memory to provide a schematic summary of brain areas involved in studies tapping visual versus verbal working memory. Results are presented in Figures 12.12, 12.13, and 12.14.

Figure 12.12 shows a schematic of brain areas—both visual from the lateral view of the brain and those tucked inside in the mesial cortex—that are active in experiments that tap working memory processes. Figure 12.13 shows activation patterns for a visual memory task, with activity in the occipital lobe as expected for an experiment using visual stimuli, and frontal lobe regions that are active due to the nature of the task. Figure 12.14 shows a similar

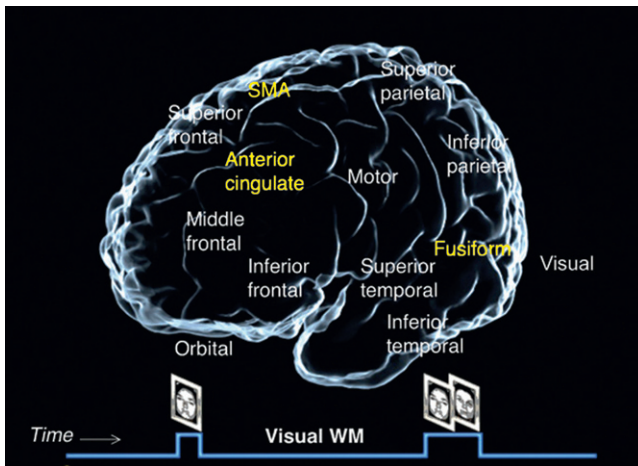


FIGURE 12.12 Outline of left cortex used in subsequent figures to mark areas activated in working memory. Areas in convexity cortex are designated with white labels, and those in mesial cortex with yellow labels. (SMA, supplementary motor area.) Below, temporal display of a trial in a typical visual working-memory (WM) task, delayed matching-to-sample, with faces. First, upward inflexion of timeline marks the time of presentation of the sample face, and second, inflexion of the choice faces. Delay-memory-period, between sample and choice, lasts 20 seconds. Source: *Fuster, 2008*.

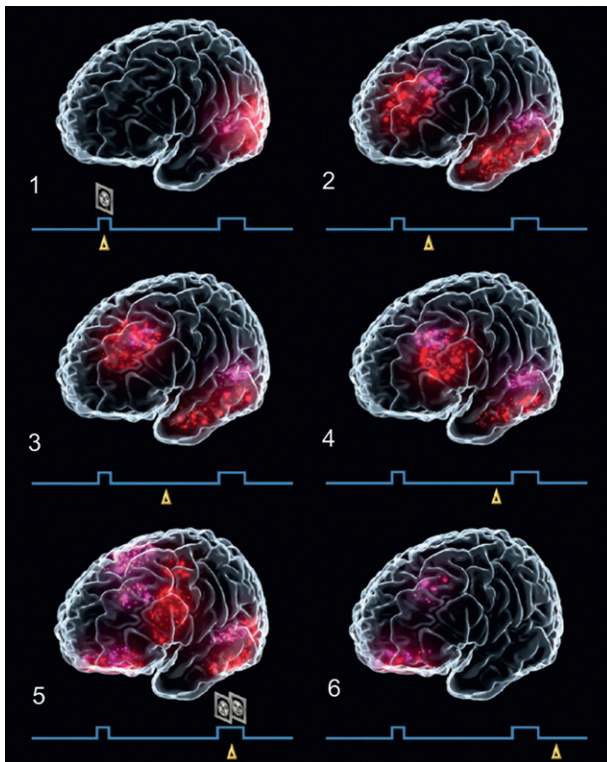


FIGURE 12.13 Relative (above-baseline) cortical activation at six moments in time (marked by yellow triangle) in the course of the visual memory task in [Figure 12.11](#). Activations of convexity cortex in red, of medial cortex in pink. (1) At the sample, the activation is restricted to visual and posterior inferotemporal cortex; (2) in early delay, it extends to lateral prefrontal cortex, anterior cingulate, anterior inferotemporal cortex, and fusiform cortex; (3) in mid-delay, it persists in prefrontal, inferotemporal, and fusiform cortex; (4) in late delay, it migrates to premotor areas, persisting in inferotemporal and fusiform cortex; (5) at the response (choice of sample-matching face), it covers visual, inferotemporal, and fusiform cortex in the back, and extends to motor areas (including frontal eye fields), supplementary motor area (SMA), and orbitofrontal cortex in the front; (6) after the trial, activation lingers in anterior cingulate and orbitofrontal cortex. Source: *Fuster, 2008*.

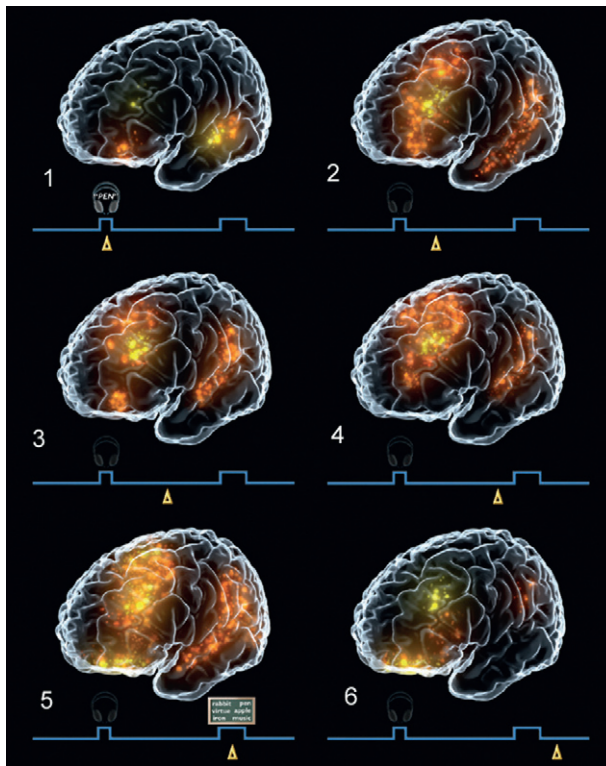


FIGURE 12.14 Cortical activation at six moments in time (yellow triangle) in the course of a verbal memory task: The memorandum, in 1, is a word through earphones. Activations of convexity cortex are in orange, and of medial or sulcal cortex in yellow. (1) At the cue-memorandum, the activation is restricted to auditory cortex, superior temporal gyrus, and inferior frontal cortex; (2) in early delay, it extends to lateral prefrontal, anterior cingulate, and superior-temporal and parietal association cortex; (3) in mid-delay, it persists in prefrontal and temporo-parietal cortex; (4) in late delay, it persists in prefrontal and migrates to premotor areas, while persisting in temporo-parietal cortex; (5) at the response (signaling whether cue word is on the screen), it covers visual and temporo-parietal cortex in the back, and extends to frontal eye fields, supplementary motor area (SMA), inferior frontal and orbitofrontal cortex in the front; (6) after the trial, activation lingers in anterior cingulate, orbitofrontal cortex, and language areas. Source: Fuster, 2008.

pattern of activation, but this time it is in response to a verbal memory task, so in this case, temporal lobe areas are active due to the auditory stimuli, along with frontal lobe regions.

One hypothesis that has been put forth about the role of working memory systems/networks in the PFC is that their function may be to *select* the material or information required for the task at hand, whereas areas in the posterior, sensory areas of the brain are involved in the actual *active maintenance* of that material or information while it is being used in a given task (see Curtis & D'Esposito, 2003, and Wager & Smith, 2003, for reviews).

4.3 Executive function and motor control

We have described a central function of the PFC as the ability to plan our actions—whether mental or physical—and then to follow out that plan. The mental planning of motor action—from initial abstract representations to the actual motor codes—takes place in the frontal lobes. A current view of the neural organization for these processes is that the more abstract representations/planning activities occur in the anterior portions of PFC, moving more posterior (and thus closer to the motor regions) as the activities become less abstract and move toward motor codes for movement (for a review, see Fuster, 2008). The level of brain activity for planning and executing complex behaviors corresponds to the level of difficulty of the

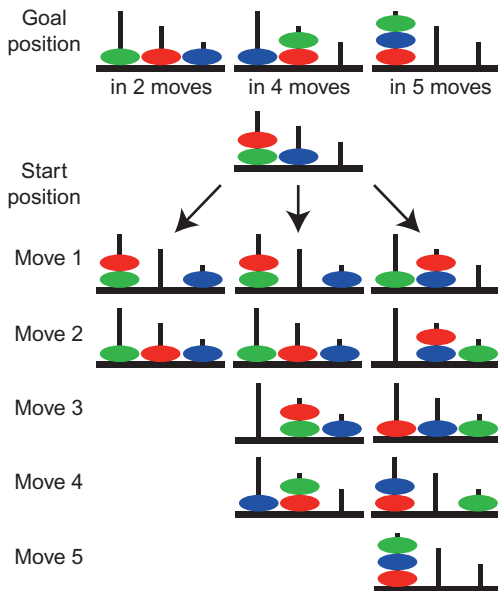


FIGURE 12.15 The Tower of London test. This task is like a puzzle with many steps for successful completion. In order to solve it, the subject needs to develop a plan. The goal position is shown at the top of the figure. Follow the moves from the Start position down through Move 5. Could you reach this Goal position with fewer moves? Source: Fuster, 2008.

action. A task frequently used to test frontal lobe executive function is the Tower of London task (Figure 12.15) (Shallice, 1982). This task is like a puzzle with many steps for successful completion. In order to solve it, the subject needs to develop a plan. Researchers have found activation in DLPFC in the left hemisphere when solving this task, with higher levels of DLPFC activation found for subjects who found the task challenging (Morris et al., 1993).

However, learning and practice change this effect, with well-learned—though complex—behaviors producing lower levels of brain activity (Figure 12.16) (Posner & Raichle, 1997; Poldrack et al., 2005). Highly automatic behaviors like tying your shoe or locking a door

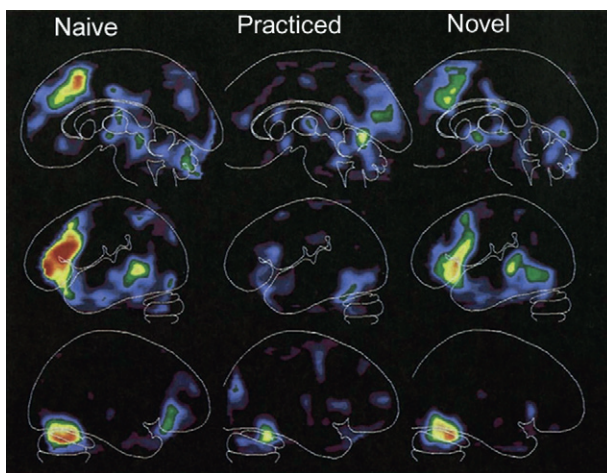
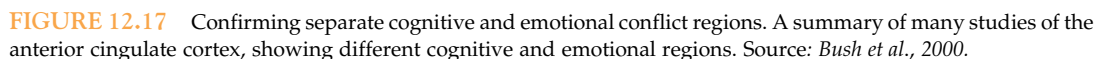


FIGURE 12.16 PET activation during performance of a verb-generation task. The subject is given a series of nouns by the investigator and required to produce a verb appropriate to each. The control task was simply the reading aloud of the names as they appeared on a TV monitor. Subtractive scans of three brain slices in three different conditions (left to right): performance by naive subject, subject practiced with the same list of nouns, and subject presented with a new list of nouns. Source: Fuster, 2008, from Posner & Raichle (1997), with permission.

We have briefly discussed the anterior cingulate cortex (ACC) (Brodmann area 24 in [Figure 12.3](#)). What is the role of the ACC in executive function? Although the role of the ACC in executive functions is still being elucidated, one hypothesis is that it has an inhibitory effect on frontal lobe processes. If this is the case, then the ACC may represent a functional part of the orbito-medial PFC that helps in reducing the effects of distracting influences on the executive planning function ([Figure 12.17](#)) (Bush et al., 2000). Fuster (2008) hypothesizes that this inhibitory control that resists distracting influences may serve as the flip side of executive attentional processes. Thus, in this way your success at focusing on a task at hand is aided both by your ability to pay attention to it and by your ability to ignore distractions.

Where do the processes underlying decision making occur in the frontal lobes? Converging evidence implicates the orbito-medial PFC, especially when there are emotional factors in the decision-making process. Think about playing a hand of poker. You must constantly make decisions about what to do next with incomplete information. Should you fold, raise, . . . what will your competitors do? In order to do well at this game, you need to assess the risk factors and the rewards. Bechara and colleagues (1994) investigated these processes using the Iowa gambling task. They and many other researchers who have investigated the neural bases for assessing risk and reward have shown that the orbital or medial PFC is activated during these tasks.



Have you ever been in a state of internal conflict over a decision that you are making? Did you feel like “part of you” wanted you to listen to your *heart* and another “part of you” wanted you to listen to your *head*? This type of internal conflict between emotional feelings and rational thoughts is proposed to reflect the trading relationship between the orbito-medial PFC, with its connections to subcortical emotional regions, and lateral PFC, with its connections to executive control regions.

4.5 Rule adoption

In order to navigate our way through our complex daily lives, it is critical to develop ways to shortcut all the things that we need to plan for and carry out. Humans are wonderful rule adopters; we develop and learn strategies for streamlining our busy lives. Like a strategic plan or a schema, rules help us increase our efficiency. The Wisconsin Card Sorting test (shown in Figure 12.18) is a good example of the mental flexibility humans have in acquiring rules and, importantly, in changing them when needed.

Neuroimaging studies of rule learning in PFC have shown that, in a manner similar to attentional and working memory demands, neural activity in the frontal regions increases with the complexity of the rule set to be learned or carried out (Figure 12.19) (Bunge, 2004).

Neuroimaging studies have shed new light on the many and diverse operations carried out—or directed—by the PFC, from paying attention to a stimulus in your environment, to monitoring how it is changing, to keeping something in mind, to complex decision making. Many of these processes are highly overlapping in time and neural regions, so we are still elucidating which frontal lobe areas contribute to these processes. Although we are still in the early stages of understanding just how and where executive processes are being done in the PFC, converging evidence from neuroimaging studies are beginning to present a clearer picture of PFC function.

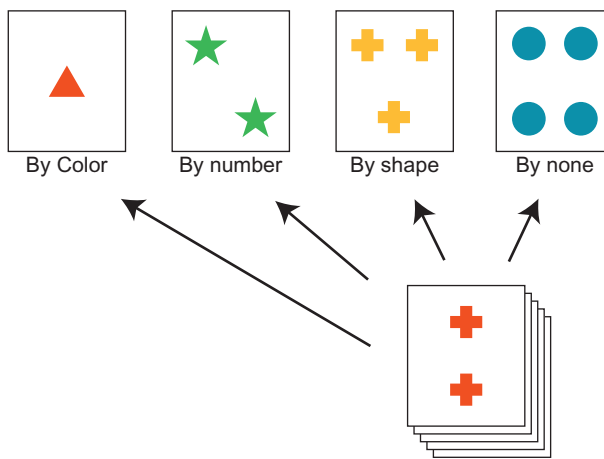


FIGURE 12.18 The Wisconsin Card Sorting Test (WCST). The cards can be sorted by matching the color of the item on the card, or the number of items, their shape, or even if they don't match on any of these features. At the beginning of the game, the experimenter determines which matching “rule” to be used (such as “match the new card by color”), but he does not tell the player the rule; the player must learn it by trial and error. During the game, the experimenter will change the rule, and again, the player must learn the new rule through trial and error. This is a test of mental flexibility: the ability to learn a new rule and to adapt to a new rule when needed. Source: Fuster, 2008.

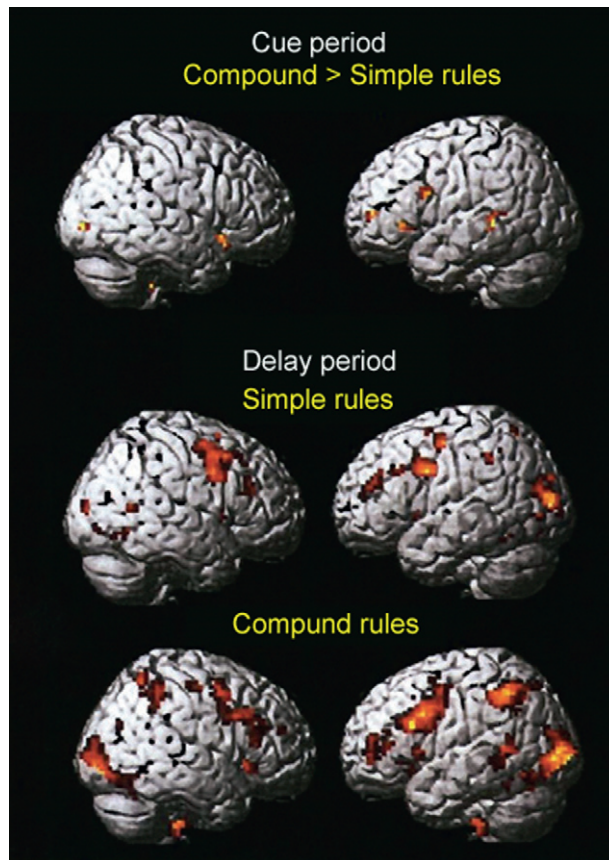


FIGURE 12.19 In this study, the experimenters wanted to see which brain areas were active while subjects implemented either simple or compound abstract “rules.” A rule cue was provided followed by a long (7–15 s) delay. Brain areas more active for compound versus simple cues are shown at the top of this figure. Areas active during the delay (while the subject is keeping the rule in mind) are shown in the middle (simple rule) and bottom (compound rule) of the figure. Source: *Bunge, 2004, as adapted in Fuster, 2008.*

5.0 DAMAGE TO THE EXECUTIVE BRAIN

We have discussed many functions of the frontal lobe, including voluntary attention, working memory, decision making, and even your personality. What happens when this critical area of the brain is damaged? Or when it fails to develop in a typical manner? The answers to these questions are as complex as the frontal lobes themselves.

5.1 The fragile frontal lobes

Frontal lobe dysfunction often reflects more than direct damage to the frontal lobes (Goldberg, 1992). The frontal lobes seem to be the bottleneck—the point of convergence of the effects of damage virtually anywhere in the brain. There is a reciprocal relationship between frontal and other brain injuries. Damage to the frontal lobes produces wide ripple effects through the whole brain. At the same time, damage anywhere in the brain sets off ripple effects that interfere with frontal lobe function. This unique feature of the frontal lobes

reflects its role as the “traffic hub” of the nervous system, with a singularly rich set of connections to and from other brain structures. This makes frontal lobe dysfunction the most common and least specific finding among neurological, psychiatric, and neurodevelopmental conditions (Goldberg, 1992).

The frontal lobes’ exceptionally low “functional breakdown threshold” is consistent with Hughlings Jackson’s concept of “evolution and dissolution” (1884). According to Jackson’s proposal, the evolutionary “youngest” brain structures are the first to succumb to brain disease. The frontal lobes’ unique vulnerability is probably the flip side of the exceptional richness of their connections. A frontal lobe dysfunction does not always signify a direct frontal lobe *lesion*. Instead, it may be a remote effect of a diffuse, distributed, or distant lesion.

5.2 Frontal lobe syndromes

The importance of executive functions can be best appreciated through the analysis of their disintegration following brain damage. A patient with damaged frontal lobes retains, at least to a certain degree, the ability to exercise most cognitive skills in isolation (Luria, 1966). Basic abilities such as reading, writing, simple computations, verbal expression, and movements may remain largely unimpaired. Deceptively, the patient will perform well on the psychological tests measuring these functions in isolation. However, any synthetic activity requiring the coordination of many cognitive skills into a coherent, goal-directed process will become severely impaired.

Damage to different parts of the frontal lobes produces distinct, clinically different syndromes. The most common among them are the *dorsolateral* and *orbitofrontal prefrontal syndromes* (Figure 12.20) (Goldberg & Costa, 1985).

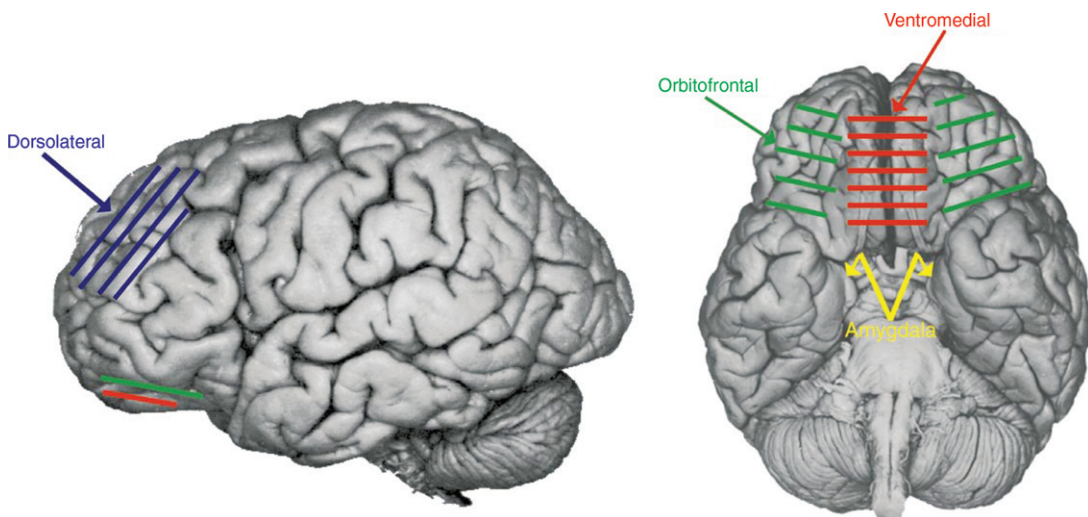


FIGURE 12.20 The orbitofrontal region is just above the orbits of the eyes. The orbitofrontal cortex (green stripes) can be distinguished in the ventral prefrontal lobe. Orbitofrontal cortex is involved in understanding future rewards, changes in reward contingencies, and goal selection. Damage to the orbitofrontal region may lead to a loss of behavioral inhibition. Source: Davidson & Irwin, 1999.

5.2.1 Dorsolateral prefrontal syndromes

Most common symptoms of dorsolateral prefrontal syndromes are *personality changes*, *high levels of distractibility*, and *mental flexibility*. Clinically, a patient with dorsolateral frontal syndrome is neither sad nor happy; in a sense, he or she has no mood. This state of indifference persists no matter what happens to the patient, good things or bad. However, the most conspicuous feature of a patient with dorsolateral syndrome is a drastically impaired ability to *initiate* behaviors. Once started in a behavior, however, the patient is equally unable to terminate or change it on his or her own. Such combined “inertia of initiation and termination” is seen in various disorders affecting the frontal lobes, including chronic schizophrenia.

Another common symptom of dorsolateral prefrontal syndromes is that the patient is at the mercy of incidental distractions and thus is unable to follow internally generated plans. In extreme cases it may take the form of field-dependent behavior. A frontal lobe patient will drink from an empty cup, put on a jacket belonging to someone else, or scribble with a pencil on the table surface, merely because the cup, the jacket, and the pencil are there, even though these actions make no sense. Easy distractibility is a feature of many neurological and psychiatric disorders, and it is usually associated with frontal lobe dysfunction. For example, *attention deficit hyperactivity disorder (ADHD)*, with its extreme distractibility, is usually linked to frontal lobe dysfunction (Barkley, 1997).

Our ability to maintain mental stability has to be balanced by *mental flexibility*. No matter how focused we are on an activity or a thought, there comes a time when the situation calls for doing something else. Being able to change one’s mindset is as important as staying mentally on track. The capacity to switch with ease from one activity or idea to another is so natural and automatic that we take it for granted. In fact, it requires complex neural machinery, which also depends on the frontal lobes. Frontal lobe damage often produces extreme mental rigidity, which may severely undermine the patient’s cognition. Quite often a closer look at a frontal lobe patient’s performance on a number of tasks shows that complete transition from one task to another is impossible, and fragments of a previous task attach themselves to the new one. This phenomenon is called *perseveration*.

5.2.2 Orbitofrontal prefrontal syndromes and self-control

The *orbitofrontal prefrontal syndrome* is, in many ways, the opposite of the dorsolateral syndrome. The patients are behaviorally and emotionally *disinhibited*. Their affect is rarely neutral, constantly oscillating between euphoria and rage, with impulse control ranging from poor to nonexistent. Their ability to inhibit the urge for instant gratification is severely impaired. They do what they feel like doing, when they feel like doing it, without any concern for social taboos and legal prohibitions. They have no foresight of the consequences of their actions. A patient afflicted with orbitofrontal syndrome may engage in shoplifting, sexually aggressive behavior, reckless driving, or other actions commonly perceived as antisocial. These patients are known to be selfish, boastful, puerile, profane, and sexually explicit. If the dorsolateral patients are in a sense devoid of personality, then orbitofrontal patients are conspicuous for their “immature” personality.

5.2.3 Reticulofrontal disconnection syndrome

In cases when the frontal lobes themselves are structurally intact but the patient presents with frontal lobe symptoms, the problem may lie with the pathways connecting frontal lobes to some other structures. Damage to these pathways may result in a condition known as the *reticulofrontal disconnection syndrome* (Goldberg et al., 1989).

The brainstem contains the nuclei thought to be responsible for the arousal and activation of the rest of the brain. A complex relationship exists between the frontal lobes and the brainstem reticular nuclei, which are in charge of activation and arousal. The relationship is best described as a loop. On the one hand, the arousal of the frontal lobes depends on the ascending pathways. On the other hand, there are pathways projecting from the frontal lobes to the reticular nuclei of the ventral brainstem. Through these pathways the frontal lobes exert their control over the diverse brain structures by modulating their arousal level. If the frontal lobes are the decision-making device, then the brainstem structures in question are an amplifier helping communicate these decisions to the rest of the brain in a loud and clear voice. The descending pathways are the cables through which the instructions flow from the frontal lobes to the critical ventral brainstem nuclei. We can easily see how damage to the pathways between the brainstem and the frontal lobes may disable executive functions without actually damaging the frontal lobes per se.

5.3 Frontal lobe damage and asocial behavior

The relationship between frontal lobe damage and asocial behavior is particularly intriguing and complex. It has been suggested, based on several published studies, that the prevalence of head injury is much higher among criminals than in the general population, and higher in violent criminals than in nonviolent criminals (Volavka et al., 1995; Raine et al., 1997). For reasons of brain and skull anatomy, closed head injury is particularly likely to affect the frontal lobes directly, especially the orbitofrontal cortex. Furthermore, damage to the upper brainstem is extremely common in closed head injury, even in seemingly mild cases, and it is likely to produce frontal lobe dysfunction even in the absence of direct damage to the frontal lobes by producing the “reticulofrontal disconnection syndrome” (Goldberg et al., 1989).

5.4 Other clinical conditions associated with frontal lobe damage

PFC is afflicted in a wide range of conditions (Goldberg, 1992; Goldberg & Bougakov, 2000), and it is not necessary to have a focal frontal lesion to have prefrontal dysfunction. The frontal lobes are particularly vulnerable in numerous nonfocal conditions. Such disorders as schizophrenia (Ingvar & Franzen, 1974; Franzen & Ingvar, 1975), traumatic brain injury (TBI) (Deutsch & Eisenberg, 1987), Tourette’s syndrome (Tourette, 1885; Shapiro & Shapiro, 1974; Sacks, 1992), and attention deficit (hyperactivity) disorder (AD(H)D) (Barkley, 1997) are known to involve frontal lobe dysfunction. Executive functions are also compromised in dementia and in depression.

5.4.1 Attention deficit (hyperactivity) disorder

The prefrontal cortex and its connections to the ventral brainstem play a particularly important role in the mechanisms of attention. When we talk about the attention deficit (hyperactivity) disorder (AD(H)D), we usually implicate these systems. Any damage to the prefrontal cortex or its pathways may result in attentional impairment. The exact causes of damage to these systems vary. They may be inherited or acquired early in life. They may be biochemical or structural. The way the diagnosis of AD(H)D is commonly made, it refers to any condition characterized by mild dysfunction of the frontal lobes and related pathways in the absence of any other, comparably severe dysfunction. Given the high rate of frontal lobe dysfunction due to a variety of causes, the prevalence of genuine AD(H)D should be expected to be very high.

6.0 A CURRENT VIEW OF ORGANIZING PRINCIPLES OF THE FRONTAL LOBES

After decades of research into frontal lobe function in nonhuman primates and in humans, using many experimental techniques and methods, some organizing principles have emerged. A leader in the field of frontal lobe research is Joaquin Fuster (2008), who proposed a model for frontal lobes function. He states the following:

1. The entirety of the cortex of the frontal lobe is devoted to the representation and production of action at all levels of biological complexity.
2. The neuronal substrate for the production of any action is identical to the substrate for its representation.
3. That substrate is organized hierarchically, with the most elementary actions at low levels of the hierarchy, in orbitofrontal and motor cortex, and the most complex and abstract actions in lateral prefrontal cortex.
4. Frontal lobe functions are also organized hierarchically, with simpler functions nested within, and serving, more global functions.

The notion of a hierarchical organization for simple versus complex, abstract versus concrete frontal lobe function has been developed in neuroimaging studies of human frontal lobe processes. A recent review article by Badre (2008) provided a summary of findings to date, including models developed by Koechlin, D'Esposito, and others, showing data supporting the view of a hierarchical organization of the frontal lobe, with an anterior-to-posterior organization that is based on the degree of abstraction (Figure 12.21).

7.0 TOWARD A UNIFIED THEORY OF FRONTAL LOBE FUNCTION

While many more details clearly need to be discovered before we have a unitary explanation of frontal lobe function, recent advances in neuroimaging techniques and methods have helped to increase our knowledge of the complex role the frontal lobes, and in particular the PFC, play in human cognition. However, even though neuroimaging studies may serve to

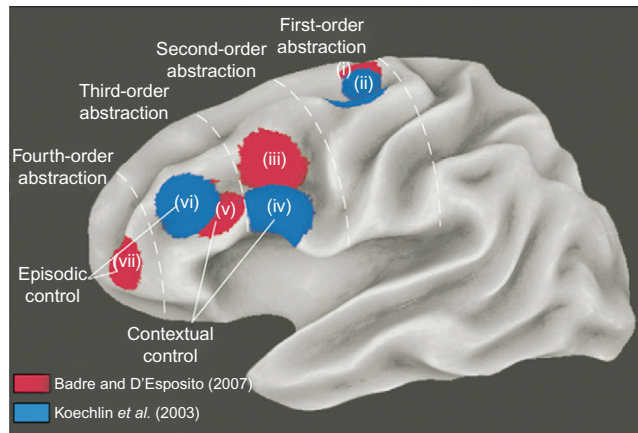


FIGURE 12.21 In a review article by Badre (2008), a proposed hierarchical organization of the frontal lobes is presented. According to this view, there is an anterior-to-posterior organization in the frontal lobes that is based on the degree of abstraction involved in the task. Moving from the front of the frontal lobes towards the primary motor areas, activity in the frontal lobes becomes less abstract and more concrete, until they relate to the planning and execution of motor related movements for performing a given task. Results from the response, feature, dimension, and context experiments and comparison to the model of Koechlin and colleagues (2003). Abstract relational hierarchy seems to provide a parsimonious account of rostro-caudal gradient across the models of Koechlin and colleagues (2003) and Badre and D'Esposito (2007). Spheres with diameters of 8 mm (within the smoothing kernel of each experiment) were centered on maxima from response (i), feature (iii), dimension (v), and context (vi) manipulations of Badre and D'Esposito (2007) (red), and on the sensory (ii), context (iv), and episodic (vi) manipulations of Koechlin and colleagues (2003) (blue). These spheres were rendered on an inflated Talairach surface. Note that the spheres are for precise illustration of proximity but do not represent actual spread of activation in each experiment. Broken lines separate manipulations at equivalent levels of abstraction in a representational hierarchy. Equivalent episodic and contextual control manipulations across the two experiments are also labeled. Source: *Badre, 2008, adapted from Badre and D'Esposito, 2007, with permission.*

guide us as to specific regions where certain executive processes—such as voluntary attention or working memory—may be located, they show a dramatically different picture of human executive function than is seen when observing a patient with frontal lobe damage. How do results from neuroimaging studies correspond to studies of patients with frontal lobe syndromes? These two sets of findings are not easy to bring together into a cohesive whole at present. Neuroimaging studies have provided a wealth of data about specific regions and locations that activate for various aspects of frontal lobe processes, but the results don't correspond directly to what we know about human behavior when frontal lobes are damaged. This is the challenge for cognitive neuroscientists: to continue to provide converging evidence across many techniques and subject groups in order to elucidate the underlying organizational principles for the complex and uniquely human PFC, the “organ of civilization.”

8.0 STUDY QUESTIONS AND DRAWING EXERCISES

1. What are some of the functions attributed to the prefrontal lobe?
2. What is the theory presented by Hughlings Jackson about evolutionarily “young” brain areas?

3. How is mental flexibility important in everyday life?
4. What type of frontal lobe damage causes mental rigidity?
5. What is one frequent way for testing mental flexibility/rigidity?
6. How do findings from neuroimaging research differ from studies of patients with frontal lobe damage?
7. Label the brain areas shown in blue, green, yellow, and pink in [Figure 12.22](#).

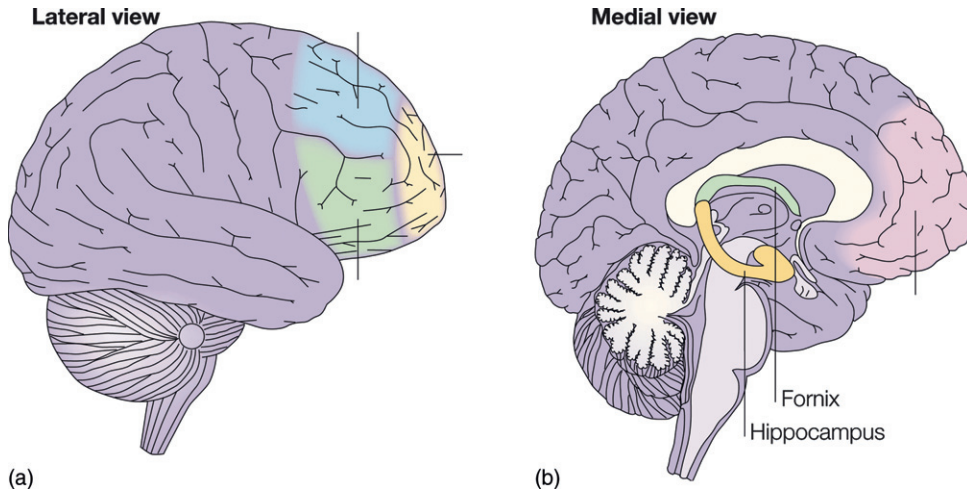


FIGURE 12.22 The major divisions of the prefrontal cortex. Prefrontal cortex can be divided into lateral (side), medial (midline), ventral (bottom), and frontal regions. The lateral division divides into upper (dorsal) and lower (ventral) halves, separated by a major horizontal fold, the inferior lateral sulcus. Source: *modified from Simons & Spiers, 2003*.

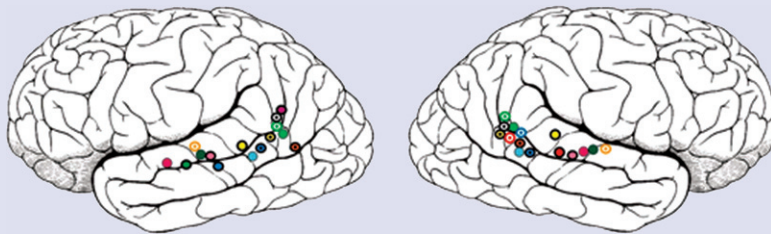
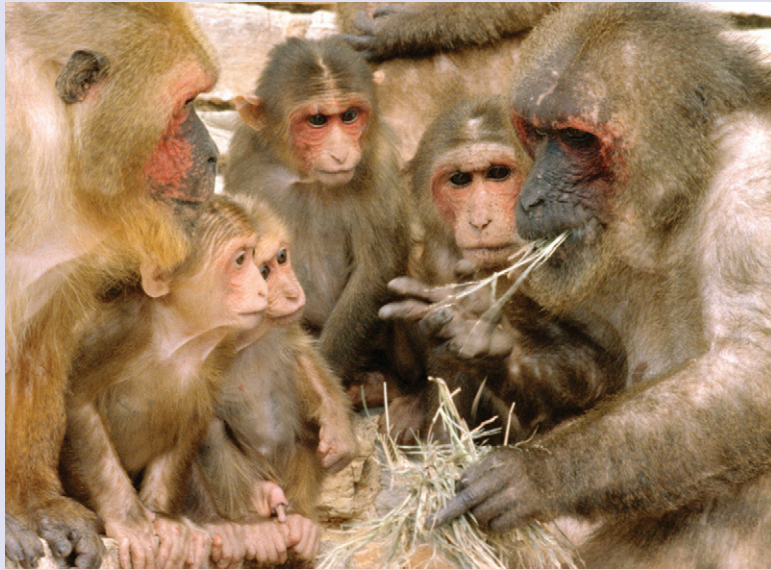
Social cognition

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Man is a social animal. *Attributed to Aristotle*

If this looks like a scene we could imagine with humans, it is because our social brains have large areas of overlap and similarity with the brains of other primates. The two cortical hemispheres in the illustration show how social cognition often activates the superior temporal sulcus (STS) in the human brain. Source: Top: *de Waal, 2004*; bottom: *Allison et al., 2000*.



1.0 OVERVIEW

Is there a social brain? Are there networks and regions in the brain that are specialized for understanding social signals—such as direct eye gaze or averting one's eyes? Are faces that display different emotions—angry versus happy, for example,—processed in the brain differently? These are questions that social cognitive neuroscientists are addressing in current research in this very new field. The advent of neuroimaging methods has helped researchers answer these questions in new and intriguing ways.

What is a social brain? These are brain regions that process important social information such as facial expressions and eye gaze. Body posture and position are also key to

understanding social cues and interpreting—and predicting—actions. The study of where these social processes are decoded in the brain is a new area of focus in this science.

The study of social cognitions seems quite different from the study of language, attention, or memory. Social cognition incorporates these aspects of human cognition, but somehow social cognition goes *beyond* each of these domains of cognition. For example, you may listen to a friend tell you a story and your brain easily decodes the sounds, words, phrases, and sentences of your native language. But you will also be recognizing the influences of intonation and facial expression to decode the “real message” being expressed. You may be paying attention to your friend as the story unfolds, but you will also be aware—sometimes unconsciously—of their body posture, eye gaze, and emotional state. And remembering your wedding day or the day you graduated from college seems much more salient—emotional—than remembering other days in your life. Social cognition spans these and other aspects of human cognition. The scientific study of brain areas that underlie these complex processes is still a new field, however much progress is being made.

1.1 Terms that are used to refer to social cognition

In the research literature, terms that refer to aspects of social cognition are often used interchangeably and in different ways by different researchers. *Empathy* carries the sense of feeling the feelings of others. In Latin, the word means “feeling inside” or “feeling with.” On the other hand, theory of mind (TOM) is often used to highlight the idea that we normally have complex metacognitive understandings of our own minds, as well as the minds of others—including cognitive and affective aspects. Similarly, Frith and Frith (1999) introduced the term *mentalizing* to capture the idea that when we have a well-developed theory of mind, we understand ourselves and others not just as sensory objects but also as subjective beings with mental states. We understand others as having mental states that we can anticipate and use to guide our own behaviors. Mind reading, like mentalizing, identifies our ability to attune our own behaviors to the minds and anticipated actions of others.

One of the most difficult aspects of the concept of theory of mind is understanding the difference between seeing others as sensory objects versus seeing others as subjective beings with minds and mental states. Having a complete TOM gives us the ability to go beyond the sensory into the mental. We can do things that those with deficient TOMs cannot do. Once we have a TOM, we can pretend, lie, deceive, guess, play hide-and-seek, and predict and understand the full range of human emotion. People who have deficits in TOM (e.g., people with autism) have limited abilities to do these things, as we will see.

Philosophers use the term *intentionality* when they want to speak about how minds and mental states are always “*about* something else” in a way that other physical objects, such as body parts, are not. Our thoughts always have an object. For example, we think “about” the chair, the book, or the idea in a way that our stomach, arm, or tooth is not about anything other than itself. Minds have mental states; minds *represent* objects and events outside themselves. It is not clear that other species comprehend the intentional nature of minds in their conspecifics. Humans seem to have an implicit understanding of the contents of others’ minds.

A separate concept is the psychological term *intention*, which is our ability to form an image of a goal state and to organize action in pursuit of that goal state. You must be careful not to confuse these two very similar terms! Theory of mind abilities allow us to read the intentions of others and to share attention with others about a common focus.

Finally, the term *intersubjectivity* emphasizes our ability to coordinate mutual interactions in light of our perception of the subjectivity and intentionality of others. When this ability is absent, we readily recognize the deficiency in the social exchanges of others. Examples are found in autistic spectrum disorders, in the sometimes deficient emotion recognition of schizophrenia, and in the empathic failures of psychopathic and borderline personalities.

1.2 Approaches to perceiving others' minds

Once past our fourth birthday (whether we are normally developing or developmentally delayed), we human beings give indications of understanding other minds—"mentalizing," as Chris Frith has called it. We can recognize and respond to the invisible, internal subjective regularities that account for the behaviors of others. We will call the full-fledged ability to understand and predict our own and others' minds *theory of mind* (TOM). TOM has been explained by three kinds of theories: module theories, theory theories, and simulation theories.

According to *module theories*, such as that of Simon Baron-Cohen, human beings develop a theory of mind module (TOMM) that is separate from but builds on other mental abilities that may be shared with nonhuman primates and other mammals; only humans are presumed to have a complete TOMM. This kind of theory fits well with findings from the study of autism.

Theory theories suppose that TOM capabilities develop as a primitive, implicit theory over the course of development, much like Piaget's conservation theories. Such implicit theories predict abrupt changes in behavior as new knowledge is added, as is seen in the abrupt change in children's understanding of their own minds between ages three and four.

Simulation theories suppose that we understand other minds by internally simulating or "running off line" the mental states of others in each situation. The dual responsiveness of mirror neurons to self- and other-generated action could be taken as support for simulation theory.

It seems very likely that all three kinds of theories are needed to account for human "mentalizing" abilities. As we will see, there are separable skills that develop in mammals and humans that operate much like *modules*; we can lose one module but still have the other. The system that allows us to imitate others seems to operate through *internal simulation* of the actions of others. Finally, adult human beings have sophisticated social perception abilities that allow us to reason about other people's internal states; we act as if we have a complex set of rules about our own and others' mental states that could be called an *implicit theory*.

2.0 AN ORGANIZING FRAMEWORK FOR SOCIAL COGNITION

Simon Baron-Cohen (1995) hypothesized that a fully developed theory of mind is composed of four kinds of skills that develop independently. These skills are *detection of intentions of others*, *detection of eye-direction*, *shared attention*, and a complex repertoire of implicit

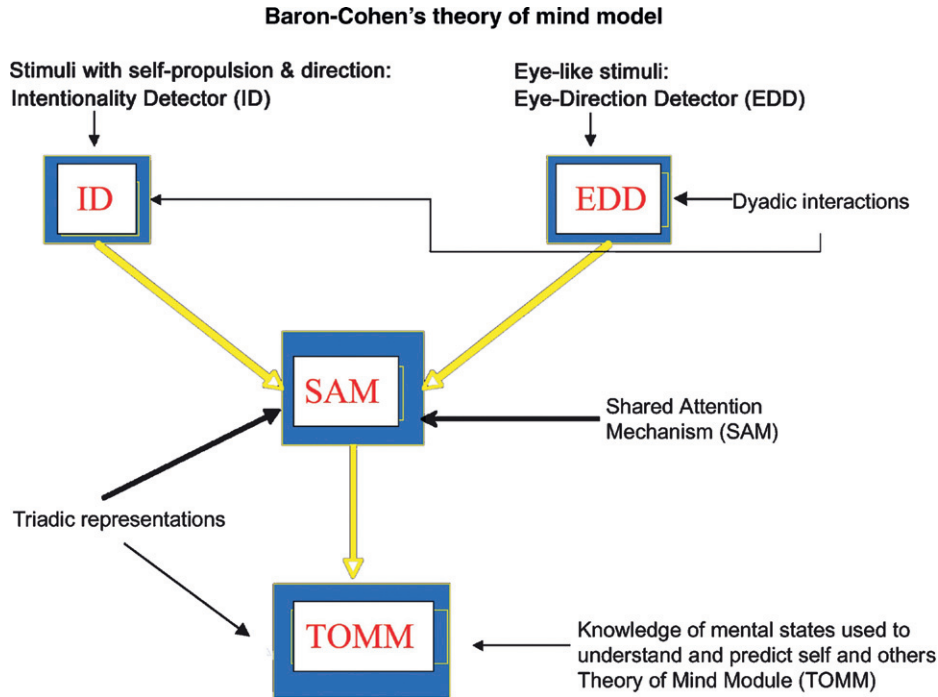


FIGURE 13.1 A schematic diagram of Baron-Cohen's theory of mind model with the eye-direction detector (EDD), shown on the upper right, sending inputs to the intentionality detector (ID), upper left, and to the shared attention mechanism (SAM), shown in the center of the diagram. The SAM also receives inputs from the ID and interacts with the theory of mind module (TOMM). Source: *Adapted from Baron-Cohen, 1995.*

knowledge about others, which he called the *theory of mind module*. Some of these skills are observed in mammals and nonhuman primates as well as in humans. However, only the theory of mind module appears in normally developing human beings. We will first introduce Baron-Cohen's model (Figure 13.1) and then use it as a way to organize the larger body of social cognition research.

2.1 Intention

The first component of Baron-Cohen's TOM is called the *intentionality detector* (ID). This is the ability to perceive intention or purposeful action in many forms of biological and nonbiological movement. For example, when we watch leaves swirling in a parking lot, we have a tendency to see the leaves as "wanting to go together." We ascribe common purpose to the pile of leaves. Or when we watch pieces of modeling clay being moved around an artificial landscape in claymation films, we readily attribute intentions and other mental states to the pieces of clay. Likewise, when we watch people and animals engaged in behaviors, we seem to understand their goals and the desired outcomes of their actions. We interpret *action* as intention.

2.2 Eye detection

The second component of the model is the *eye-direction detector* (EDD), which is the skill to detect eyes and eyelike stimuli and to determine the direction of gaze. Many mammals seem to have the ability to notice and use information about eye direction. Cats, for example, use eye direction as part of their social dominance behavior with other cats; the nondominant cat must avert its eyes in the face of the dominant cat. Humans, from the first hours of life, search for and focus on the eyes of their caregivers. We also have a strong tendency to see nonliving stimuli as eyelike; hence, we see the “man in the moon” and faces on automobiles, gnarled trees, and mountains. The “language of the eyes” seems to be a fundamental means of communicating mental states among humans.

Both the intentionality detector and the eye-direction detector involve *dyadic* (two-way) interactions. That is, there is *one perceiver* and *one object of perception*. As yet, no sharing of mental states is necessarily involved. Both EDD and ID are found in nonhumans as part of their social perception abilities. It is the third module of TOM that is unique to human social cognition.

2.3 Shared attention mechanism

The *shared attention mechanism* (SAM) is the ability we have by the end of our first year of life to understand that when someone else shifts his or her direction of gaze, he or she is “looking at” something. We seem to learn that looking leads to seeing—an advance over the simpler

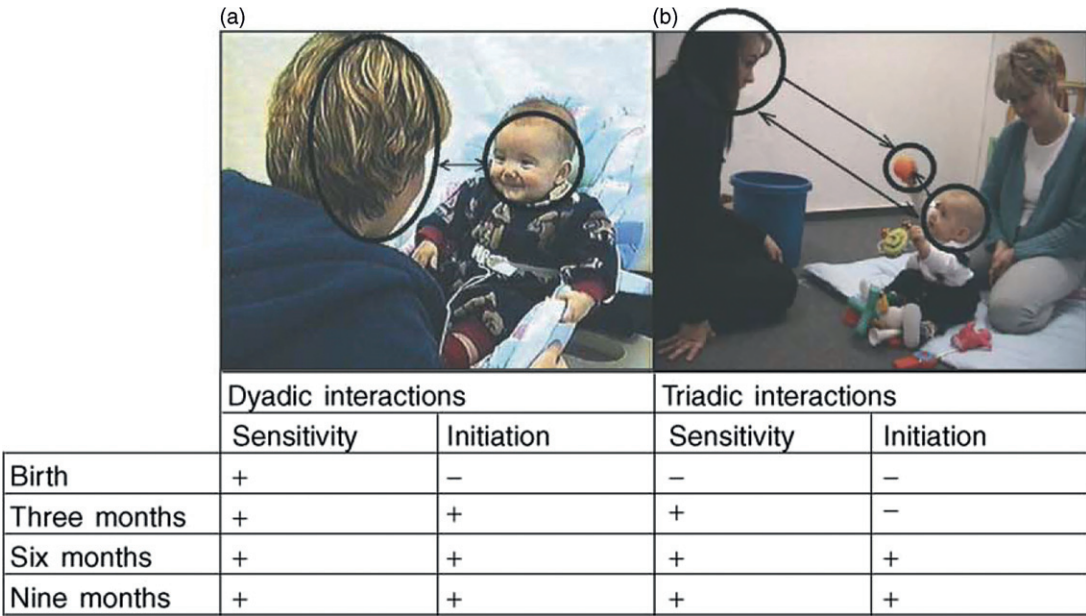


FIGURE 13.2 There is a developmental progression in the sensitivity of infants to dyadic (2-way) and triadic (3-way) social interactions. (a) Dyadic (person-to-person) exchange. (b) Triadic (person-object-person) exchange. The plus (+) sign indicates evidence for that skill (dyadic or triadic exchange) and the minus (–) sign indicates no evidence for that skill. Source: *Striano & Reid, 2006*.

signal of eye direction. We realize that we can look, too, and see the same thing. Gaze shifting and social pointing of fingers are ways we learn to direct the attention of a companion.

Infants before 1 year of age, most other primates, and other mammals do not have a shared attention ability. We can see this in our much-loved companion animals. While our family dog may chase a ball and bring it back, he will not follow our gaze if we look toward a ball lying in the grass. He will not follow our pointing finger when we try to direct his gaze toward the ball. The dog has considerable intelligence but does not have shared attention. Similarly, an infant at 6 months does not turn her head to follow the caregiver's gaze, but a 1-year-old does. Shared attention abilities mark the human species (Figure 13.2).

2.4 Higher-order theory of mind

The final component of full-fledged theory of mind is what Baron-Cohen has called the *theory of mind module* (TOMM), a complex knowledge base containing rules of social cognition that develops by the time we reach our fourth birthday. TOMM tells us that:

- Appearance and reality are not necessarily the same: A rock can look like an egg but not be an egg; I can pretend to be a dog but not be a dog.
- A person who is sitting still in a chair may be “doing something”—that is, thinking, imagining, or remembering (young children do not appreciate this).
- Other people can have mental states as well as physical states.
- Other people can know things that I don't know: I can be fooled or deceived. I can detect deception.
- I can know things that other people don't know: I can fool or deceive others. I understand the point of games like hide-and-seek.
- My mental state in the past was different from how it is now.
- Facial expressions are indicators of mental states as much as they are indicators of physical states: I can distinguish a surprised face from a yawning one.

TOM is not the same as intelligence or IQ. Developmentally delayed children and adults display complete TOM abilities despite low IQs, while people living with autistic spectrum disorders (ASD) may have high IQs but markedly deficient TOM abilities. We can now use Baron-Cohen's four TOM skills as a way to organize and guide our study of social cognition.

3.0 SOCIAL COGNITION IN THE BRAIN

3.1 Intention

You see your roommate come out of his room wearing sweatpants, a t-shirt, and running shoes. He is resetting his watch. Ah, you think, he is going for a run. But how do you know his intention based on the simple actions of his leaving a room and setting a watch? Understanding intentions is a key aspect of action perception and humans are amazingly adept at it. Converging evidence from animal studies using single-cell recordings and human neuroimaging studies implicate the posterior part of the Superior Temporal Sulcus (pSTS) in interpreting actions (for a review, see Nummenmaa and Calder, 2009). In one study, researchers



FIGURE 13.3 Keeping the visual stimulus—a human face with the eyes gazing to the side—the same, researchers investigated the effects of the eyes gazing toward a visual checkerboard or away from it. A region in the pSTS (b) responded to the intentionality of gaze shifts for typical individuals (b) but not for individuals on the autism spectrum (c). Source: Nummenmaa & Calder, 2009.

investigated the intentionality of gaze shifts and found that pSTS responded to the intentionality of gaze shifts (Figure 13.3).

3.2 Eye detection and gaze perception

Perception of eyes in conspecifics (individuals of the same species: such as human-human, dog-dog) and guiding of social behavior in light of that perception occurs in many classes of animals from reptiles to humans. While fish, reptiles, birds, and other mammals have some ability to process eyelike stimuli and perceive gaze direction, only great apes (gorillas, chimpanzees, bonobos, and orangutans) and humans have shared attention and can use the “language of the eyes” to understand the mental states of others.

Several types of eye and gaze processes are shown in Figure 13.4. In the first example ((1) left), mutual gaze is shown where two individuals are making direct eye contact. In some animals, this type of direct eye contact can be threatening. In humans, however, direct eye contact and mutual gaze are important bases for social communication (see the review by Senju & Johnson, 2009).

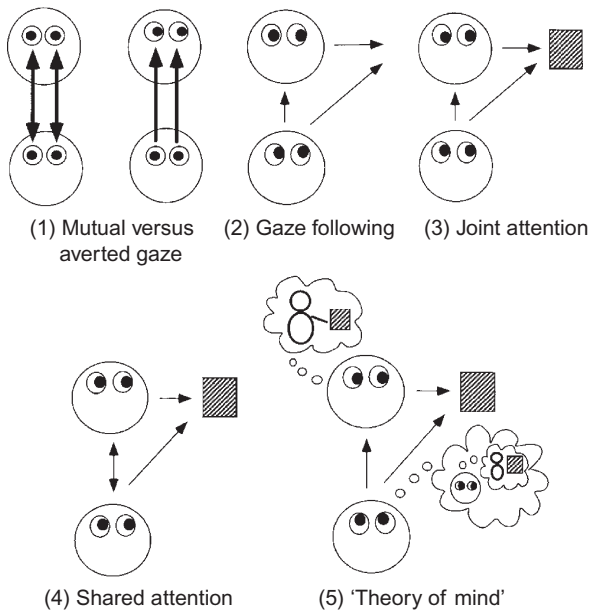


FIGURE 13.4 Eye and gaze processing. (1) Mutual gaze is where the attention of individuals A and B is directed to each other. Averted gaze is when individual A is looking at B, but the focus of B's attention is elsewhere. (2) Gaze following is where individual A detects that B's gaze is not directed toward him and follows the line of sight of B to a point in space. (3) Joint attention is the same as gaze following except that there is a focus of attention (an object) so that individuals A and B are looking at the same object. (4) Shared attention is a combination of mutual attention and joint attention, where the focus of attention of A and B is on an object of joint focus and on each other ("I know you're looking at X, and you know I'm looking at X"). (5) Theory of mind relies on 1–4 as well as higher-order social knowledge that allows individuals to know that the other is attending to an object because that person intends to do something with the object. Source: Emery, 2000.

Where do these processes take place in the brain? The superior temporal sulcus registers eyes and eyelike stimuli. The more complex levels of gaze processing (gaze direction and detection of gaze aversion) involve connections between STS and areas in the parietal lobe, particularly the intraparietal sulcus (IPG) (Figure 13.5) (Haxby et al., 2000). In addition, connections of STS and IPG with subcortical structures, such as the amygdala, allow us to register the social and emotional significances of gaze, including threat.

Social information from eyes and gaze direction come from the *changeable aspects of the human face*. We can also use visual information to detect the *invariant aspects of individual faces*, such as identity. These aspects of face perception occur in a separate area of the temporal cortex.

3.3 Shared attention

Shared attention seems to be a social skill that is unique to great apes and humans. Remember that shared attention is more than simply looking at the same thing that another person is looking at. Shared attention involves the additional qualification that the two observers not only observe the same object but also know that the other is looking at the object. It is a triadic (three-way) activity. Shared attention allows us implicitly to recognize that "I know that *you* are looking at *that*." Apes and humans seem to know that when conspecifics are gazing at something, they are also internally representing it. Looking leads to seeing. If I want to see what you see, I can follow your gaze (Box 13.1).

How do these shared processes get set up in humans? Brooks and Meltzoff (2003) have shown that human infants begin to follow the direction in which an adult turns his or her

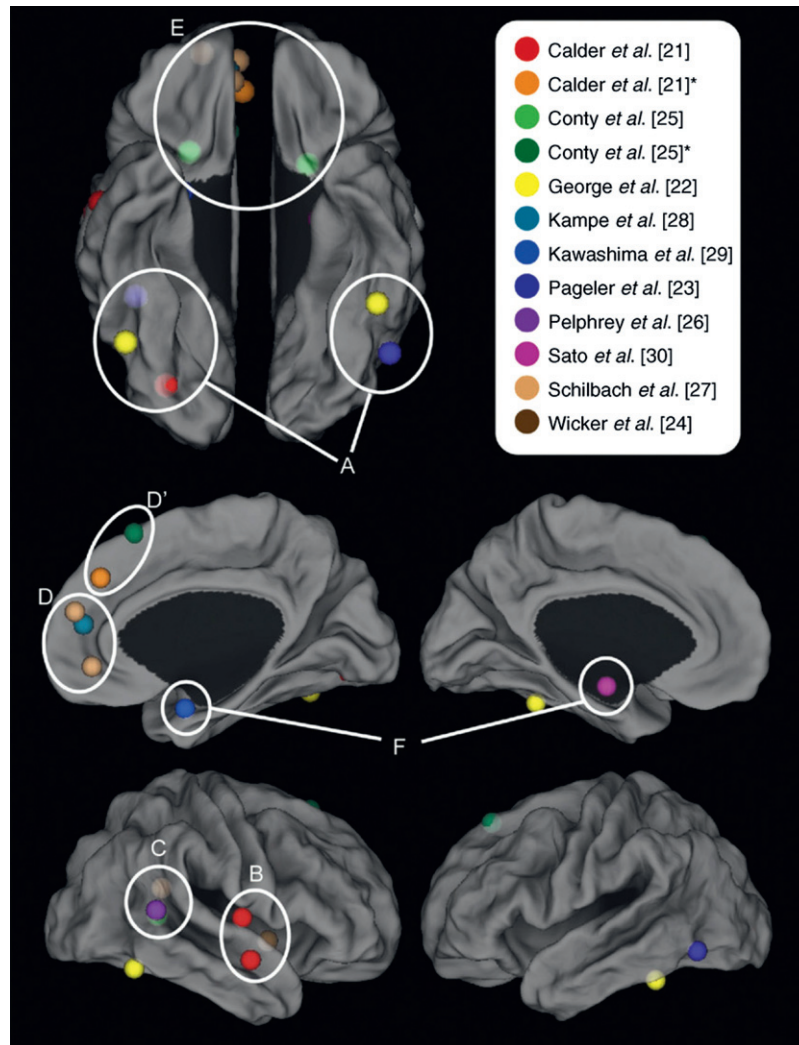


FIGURE 13.5 Brain regions for eye gaze perception. Amassed from many studies of eye gaze perception, this figure shows some of the regions that reflect eye detection and gaze perception in the social brain. Source: *Senju & Johnson, 2009*.

BOX 13.1

GAZE-FOLLOWING EXPERIMENT

Try this experiment with shared attention. When you are in a gathering of friends or classmates, shift your gaze to the corner of

the room without saying anything. See whether others follow your gaze. Ask them why they did what they did.



FIGURE 13.6 An 18-month-old pointing. Pointing is a sign of triadic interaction. Source: *Brooks & Meltzoff, 2003*.

head by the age of 9 months; however, at 9 months, the infant follows head direction whether the model's eyes are open or closed. By 12 months of age, the infant will follow gaze more often when the model's eyes are open than when they are shut. The infant follows gaze rather than head direction now. Shared attention has developed. The infant seems to know implicitly that open eyes allow looking, and looking leads to seeing (Figure 13.6).

What areas of the brain support shared attention? We know that STS supports eye detection. In order to move from simple detection to shared attention, areas in the prefrontal cortex become involved. Williams and colleagues (2005) studied adults when they were experiencing shared attention compared to a control condition (Figure 13.7).

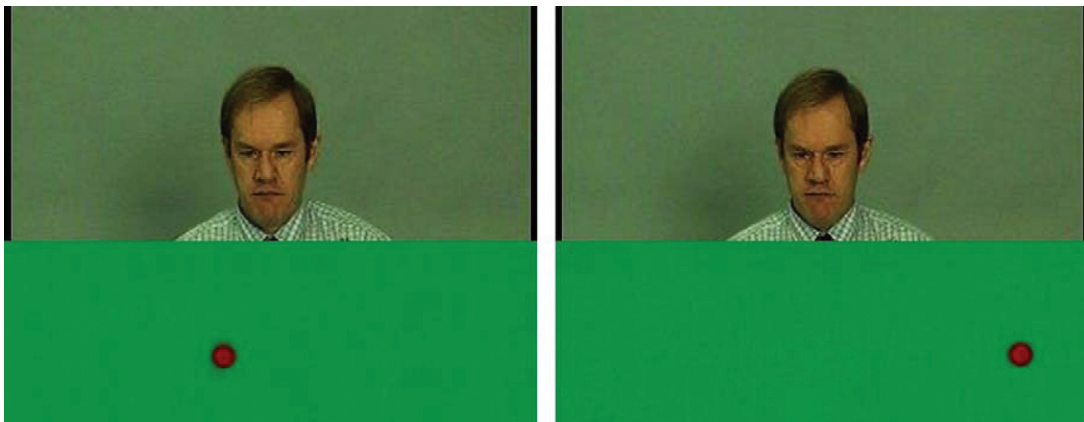


FIGURE 13.7 Stimuli used to create joint attention. When we look at the red dot on the left, we have the sense that the man is looking at the same object as we are. Looking at the red dot on the right does not lead to the same sense of shared attention. Source: *Williams et al., 2005*.

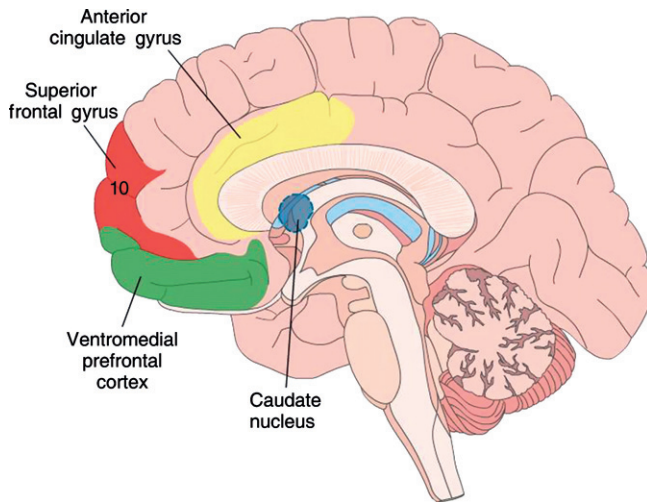


FIGURE 13.8 Networks for shared attention.

Images from fMRI analyses show that shared attention recruits frontal areas, including the ventromedial prefrontal cortex (VM-PFC), the left superior frontal gyrus (BA 10), the cingulate gyrus, and the caudate nucleus. The VM-PDF is associated with registering the mental state of the other, as we will discuss next. Williams and colleagues speculate that BA 10 is responsible for matching perception and action ([Figure 13.8](#)).

3.4 Higher-order TOM abilities

3.4.1 Attribution of mental states to ourselves and others

In the previous sections, we found that the paracingulate is involved in imitation learning and that the ventromedial prefrontal cortex (VM-PFC) is involved in shared attention. In this section, we examine the role that the medial wall of the PFC plays in attribution of mental states to others, or, as Chris Frith calls it, “mentalizing.”

The medial wall of prefrontal cortex can be divided into three segments from top to bottom: dorsomedial prefrontal cortex (DM-PFC), medial prefrontal cortex (M-PFC), and ventromedial prefrontal cortex (VM-PFC). (They are divided by convention according to their Talairach coordinates in 3D space, which we will not worry about here.) DM-PFC includes the cortex at the top of the medial wall of the prefrontal cortex. M-PFC is the middle section of the medial wall of PFC. VM-PFC is composed of the bottom of the prefrontal lobe and the lower inside wall of the prefrontal cortex ([Figure 13.9](#)).

The cingulate and paracingulate gyri, which are sometimes spoken of collectively as the anterior cingulate cortex (ACC), form a belt (*cingulum* in Latin) around the corpus callosum. In addition, depending on how the gyri of individual brains are folded, the paracingulate gyrus may be folded into a sulcus. [Figure 13.10](#) helps us see the anatomy of the cingulate and paracingulate gyri. [Figure 13.11](#) depicts brain areas active for perspective taking and intentional stance.

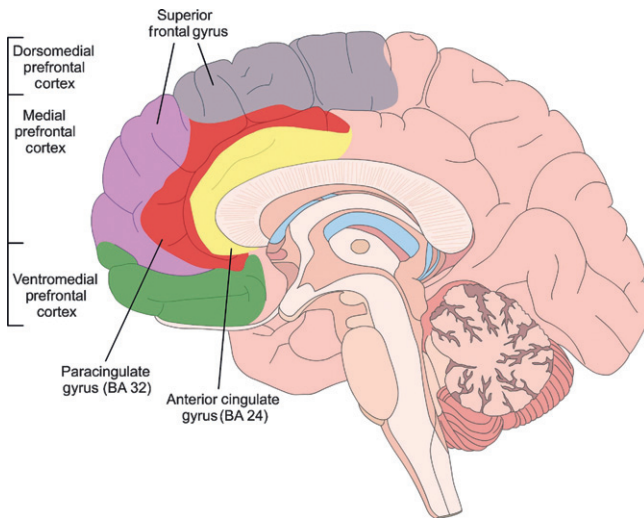


FIGURE 13.9 Divisions of prefrontal cortex: DM-PFC, M-PFC, and VM-PFC. Superior frontal gyrus, cingulate (BA 24), and paracingulate (BA 32) are areas shown to be important in attribution of mental states.

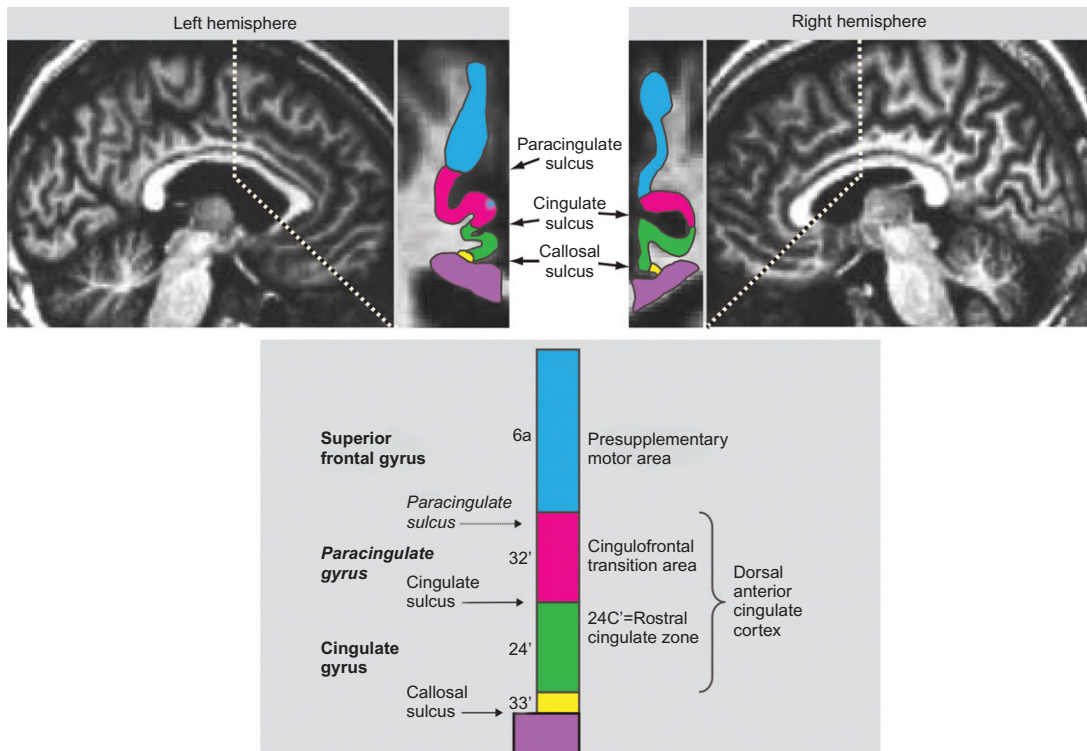


FIGURE 13.10 Anatomy of cingulate and paracingulate gyri: the upper left panel shows the left hemisphere and the upper right panel shows the right hemisphere. The paracingulate sulcus is shown in blue, the cingulate sulcus is shown in pink, and the callosal sulcus is shown in purple. The lower panel shows these regions in more detail, including the rostral portion of the cingulate zone. Source: *Heckers et al., 2004*.

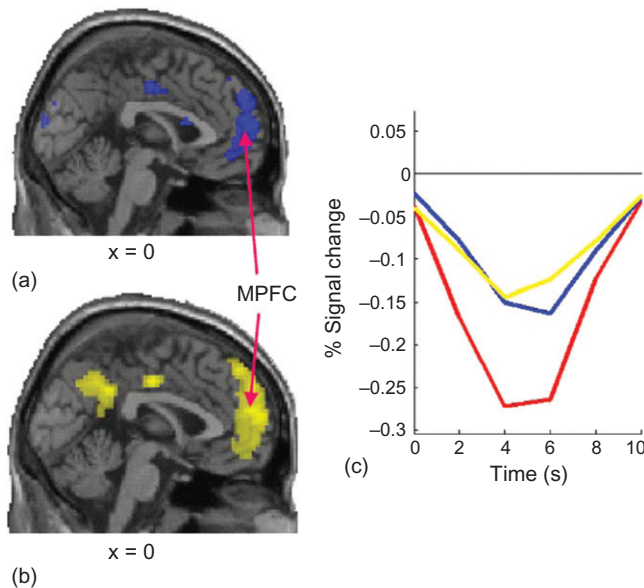


FIGURE 13.11 Perspective-taking and intentional stance. (a) Significant medial prefrontal activation for self versus artificial pain. (b) Significant M-PFC activation for other versus artificial pain. (c) Change in regional blood flow in the PET procedure in M-PFC; self = blue line; other = yellow; artificial limb = red. Source: Jackson et al., 2006.

3.4.2 Perspective taking and intentional stance

Perspective taking is a social skill that is fundamental to human empathy. It allows us to understand how another person thinks and feels about a painful situation. For example, when people are asked to imagine the pain that they or another person would feel (compared to how an artificial limb would feel) when their fingers are pinched in a car door, the medial prefrontal cortex is significantly activated as well as other cortical areas associated with pain perception (Jackson et al., 2006). Specifically, the paracingulate (BA 32) cortex of the M-PFC is significantly activated in both perspectives; it registers imagined self and other pain. In addition, when participants were imagining their own pain, the cingulate cortex (BA 24) was also active. This difference reflects our ability to empathize with the pain of others but also to distinguish our own pain from theirs.

Or consider playing a game with another person. Gamers and athletes speak of “psyching out” their opponent. A lot of what they mean is that they read the other person’s mind. To do this, we put ourselves in the other person’s shoes, or, to say it another way, we use empathy. When we play the game “Rock, Scissors, Paper” against an unseen person (compared to an unseen computer), we adopt an intentional stance. We act as if the opponent is another subjective being. And we can see a difference in the metabolic activity of the brain that coincides with our adoption of an intentional stance. In Figure 13.12, we can see that the anterior paracingulate cortex (BA 32) is activated—that part of the medial prefrontal cortex implicated in perception of mental states in ourselves and others (Gallagher et al., 2002).

We are sometimes asked to make decisions for others, keeping in mind what they would want. In a study where medical students were asked to adopt the perspective of a patient in order to make putative health care decisions for them, PET scans again revealed unique medial frontal activity—in this case, in the medial superior frontal gyrus (Figure 13.13) (Ruby and Decety, 2003).

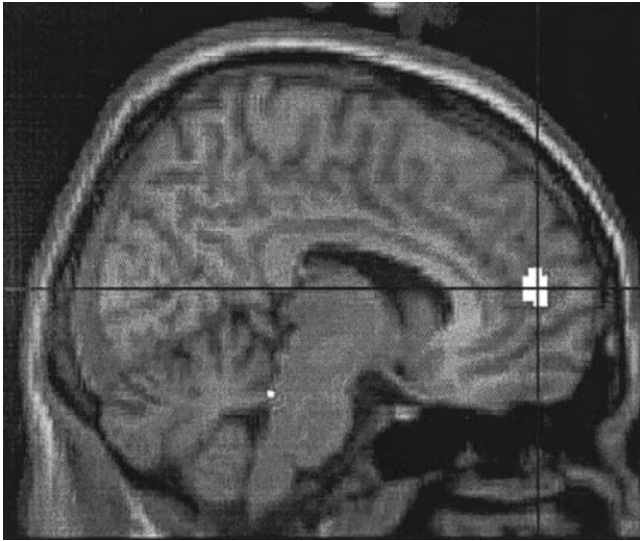


FIGURE 13.12 Activation in anterior paracingulate cortex when we mentalize about our opponent. Source: *Gallagher et al., 2002*.

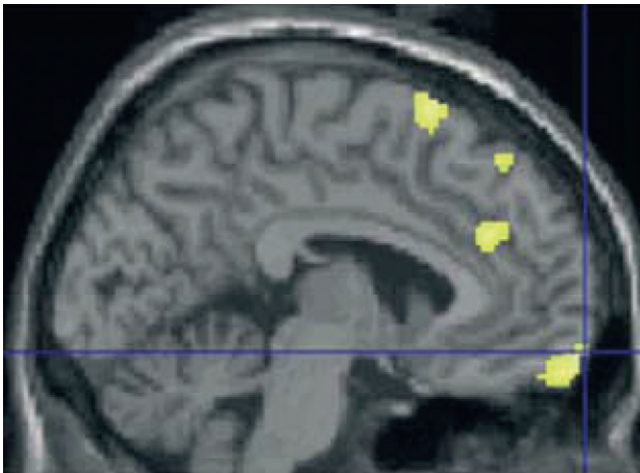


FIGURE 13.13 Adopting the perspective of another to make health care decisions for him or her. Medial PFC activation appears in yellow toward the right. Source: *Ruby & Decety, 2003*.

3.5 Face perception

Perception of the unchanging aspects of the human face occurs in the fusiform face area (FFA), which is part of the inferior temporal lobe ([Figure 13.14](#)). As an example of how the FFA looks in a brain image, we can look at the PET/MRI image from Caldara and colleagues (2006) ([Figure 13.15](#)). These researchers compared cortical activation when participants observed objects versus human faces. In the image, we are looking at the bottom of the brain. The temporal lobes take up most of the outside areas of the image. The right and left FFAs are clearly marked in red, showing face receptive areas. Next to the FFAs are other parts of the

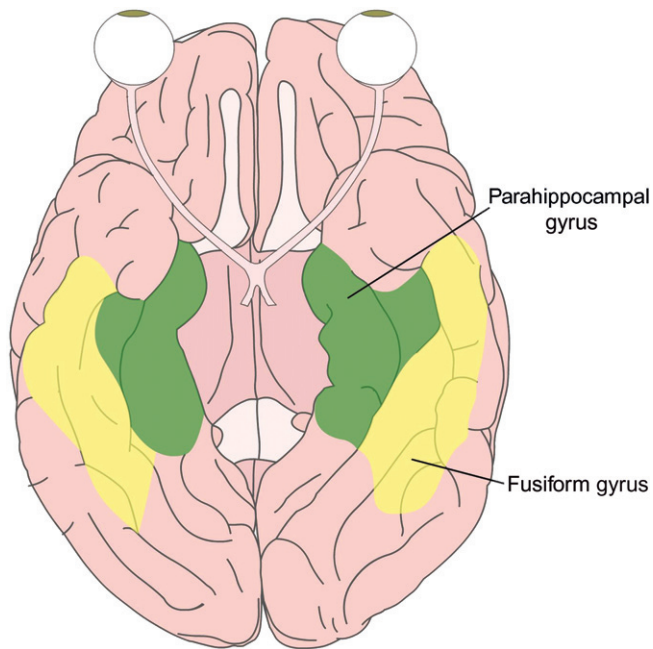


FIGURE 13.14 View from the underside of the theme brain, showing where the fusiform face area (FFA) is located.

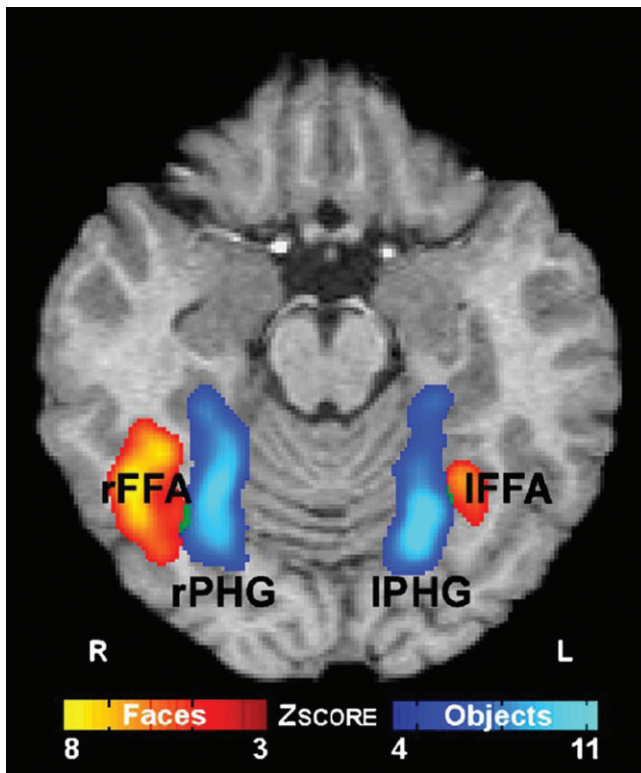


FIGURE 13.15 A view of the underside of the brain with fusiform face areas (FFA) shown in red and parahippocampal gyri (PHG) shown in blue. Source: *Caldara et al., 2006*.

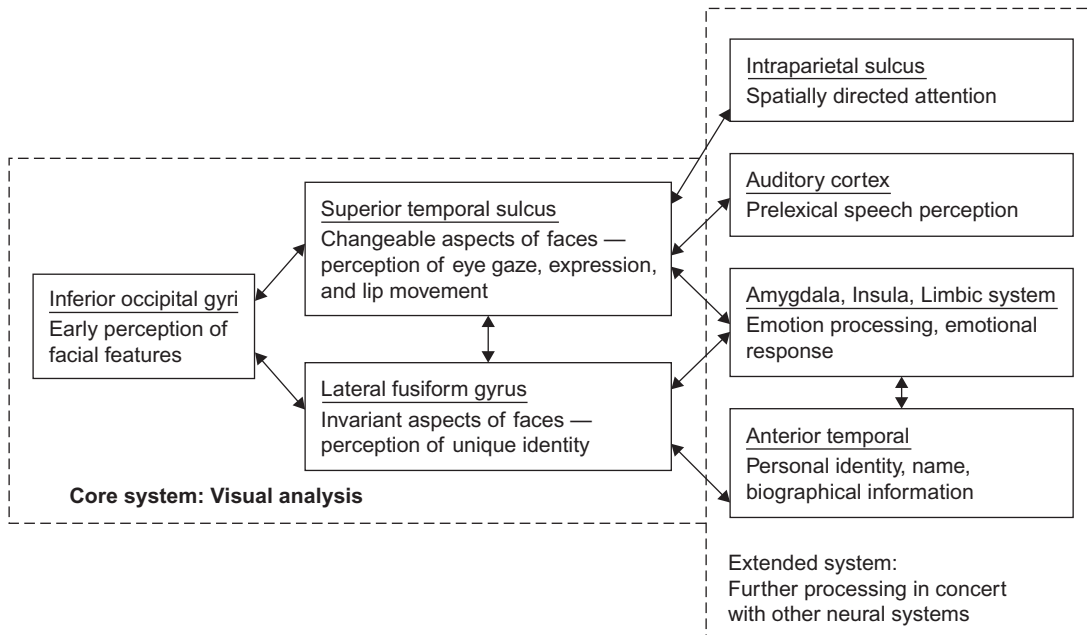


FIGURE 13.16 Model of facial perception developed by Haxby and colleagues. The left side of the model shows early visual regions for face perception, the center shows brain regions for changing and nonchanging features in faces, and the right side shows further processing of facial features. Source: *Haxby et al., 2002*.

inferior temporal lobe: the right and left parahippocampal gyri (PHG) that respond to inanimate objects, such as houses or shoes.

Haxby and his colleagues (2002) put the results of numerous studies together to create a model of face perception areas in the brain (Figure 13.16). They proposed a hierarchical system of interconnected brain areas to account for both the changeable and invariant aspects of face perception that have been discussed in this chapter.

In this model, early visual analysis of facial features occurs in the visual cortex, inferior occipital gyrus (IOG). The IOG sends information to the superior temporal sulcus (STS), where changeable aspect of faces, such as eyes, are processed; from there, information about eyes is joined with spatial information in the intraparietal sulcus (IPS) to generate gaze direction information. Information from STS can also be sent to the amygdala, where social and affective meanings are attached and to the auditory cortex where lip movements are registered. Invariant aspects of faces such as personal identity are processed in the lateral fusiform gyrus (the FFA) that is interconnected with the temporal lobe, where specific information about name and biographical data are retrieved.

3.6 The social brain network

In summary, we have described many brain areas that are involved in social cognition. To recap, the social brain network includes both cortical and subcortical regions of the brain. Specifically, they include the prefrontal cortex, the superior temporal gyrus, the fusiform gyrus, the cingulate gyrus, and the amygdala (see Senju & Johnson, 2009, for a review).

4.0 EMOTION AND THE SOCIAL BRAIN

Emotions play a huge role in social behavior. Indeed, it is difficult to separate aspects of emotional and social processing. While face perception is a key social ability, the interpretation of the emotional aspects of that face is equally important for the social scene. In this section, we briefly lay out the evidence for brain areas that are involved in processing emotional situations. The best-studied emotion in animal studies is fear, so we shall begin there. In humans, other aspects of emotion + social cognition have been the focus of study, including emotional perception, emotional memories, and rewards. First, however, let's review some definitions of an emotional system. Jaak Panksepp (1998) offered a functional definition of an emotional system in the brain (Figure 13.17):

1. The underlying circuits are genetically predetermined to respond unconditionally to stimuli representing evolutionary pressures faced by the species.
2. The circuits organize motor programs and autonomic and hormonal changes to respond to the environmental challenge or opportunity at hand.
3. The circuits tune sensitivities of sensory systems to be responsive to stimuli relevant to the emotion evoked.
4. The positive feedback of neural activity means emotional arousal outlasts the precipitating circumstances.
5. Emotional circuits can come under cognitive control.
6. Emotional circuits reciprocally influence higher decision making and appraisal systems and consciousness.
7. The circuit is capable of elaborating distinctly difference subjective feelings (not shown in Figure 13.17).

Panksepp (1998) described a small set of “hard-wired” emotion systems found in mammalian brains. (We will follow Panksepp's convention of identifying the systems by capitalized labels; the capital letters remind us that we are speaking of systems of emotion and not simply the conscious feelings associated with the systems or single brain locations.) The first four emotion systems appear shortly after birth in all mammals:

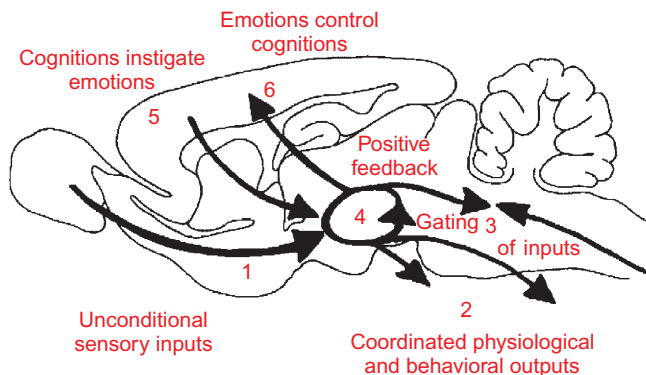


FIGURE 13.17 The functions of emotional systems: (1) unconditioned sensory inputs, (2) coordinated physiological and behavioral outputs, (3) gating of inputs, (4) positive feedback, (5) cognitions instigating emotions, and (6) emotional control over cognitions. Source: Panksepp, 2006.

- **SEEKING:** the appetitive system that makes mammals curious about their world and promotes goal-directed behavior toward a variety of goal objects, such as food, shelter, sex
- **FEAR:** the system that responds to pain and the threat of destruction and leads to the well-known flight, fight, or freeze behavior
- **RAGE:** the system that mediates anger and is aroused by frustration, bodily irritation, or restraint of free movement
- **PANIC:** the system that responds to separation of young animals from their caregiver by activating crying and separation calls

These four emotional systems and their mutually inhibitory or excitatory relationships with one another are illustrated in [Figure 13.18](#).

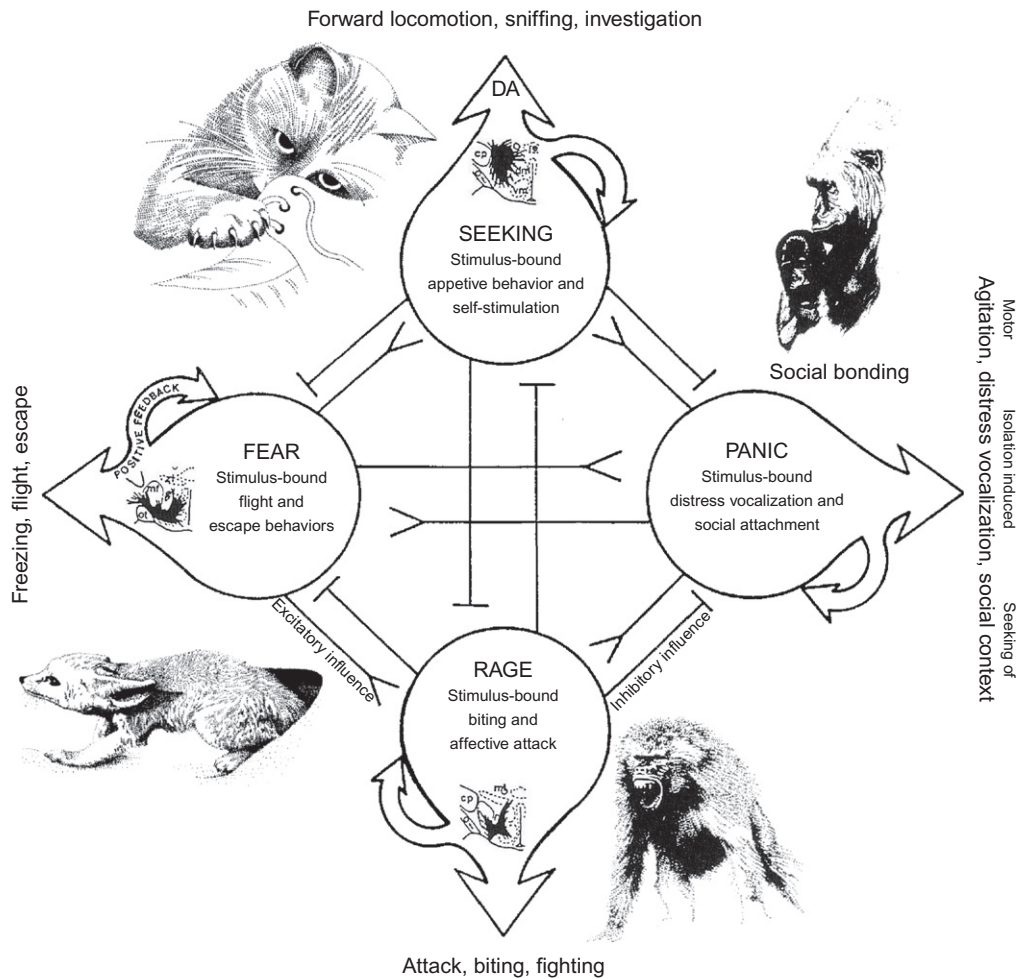


FIGURE 13.18 Four fundamental mammalian emotional systems, shown with prototypical behaviors. Source: Panksepp, 1998.

4.1 Fear processing

The fear system is a neural system for avoiding pain or injury. It is based primarily in the central and lateral nuclei of the amygdala with connections to the medial hypothalamus and dorsal periaqueductal gray matter (PAG) of the midbrain. This system responds to both unconditioned stimuli (loud sounds, looming and sudden movements, painful stimuli, fearful faces) and conditioned stimuli (classically conditioned danger signals, memories, images) arriving from the thalamus and sensory and association cortices (Figure 13.19). Reciprocal efferent pathways return feedback signals to these thalamic and cortical sites to tune sensory processing in emotion-specific ways (Figure 13.20). It is clear that the efferent (outgoing) pathways *from* the amygdala to the cortex are as complex and rich as the afferent (incoming) pathways *from* the cortex *to* the amygdala.

4.1.1 Conscious and unconscious fear processing: LeDoux's high road and low road

LeDoux (1996) labeled the two sensory input pathways to the amygdala for perception of fearful stimuli the "low road" and the "high road." The low road is a fast pathway from sensory receptor to sensory thalamus to the amygdala that bypasses the cerebral cortex (Figure 13.21). The direct thalamo-amygdala (low road) processing is only capable of low spatial resolution of stimuli and thus can respond only to simple stimuli or to the gross characteristics of complex stimuli. This "quick and dirty" processing enables automatic, unconscious reactions to the broad outlines of potentially dangerous stimuli before we have to time to think about our responses.

The longer thalamo-cortico-amygdala pathway (high road) takes somewhat longer to traverse but allows complex, contextualized processing of stimuli, followed by conscious, deliberate

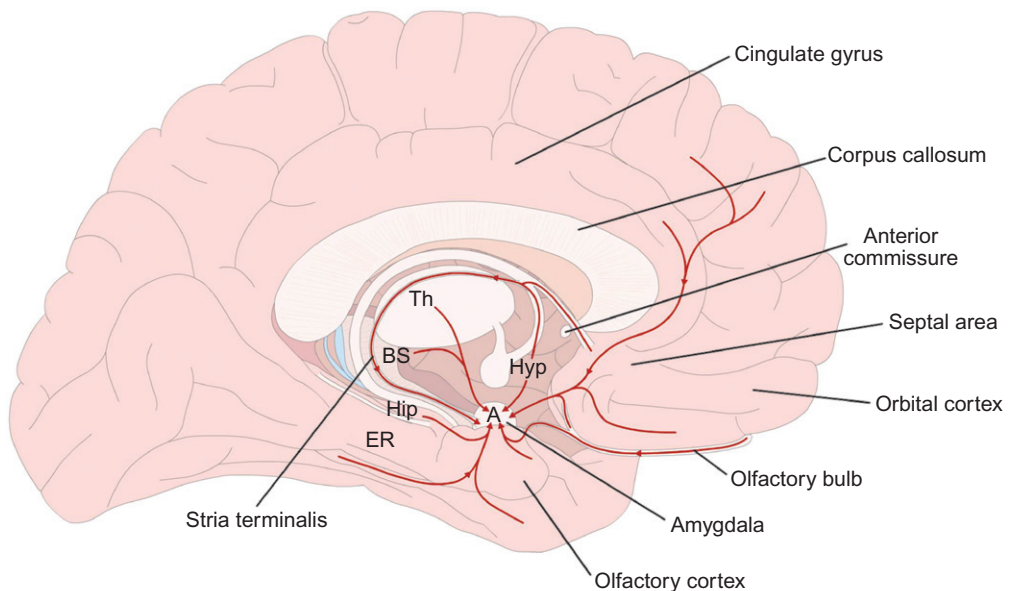


FIGURE 13.19 Afferent pathways to the amygdala. Hip 5 hippocampus; BS 5 brainstem; Th 5 thalamus; Hyp 5 hypothalamus; A 5 amygdala.

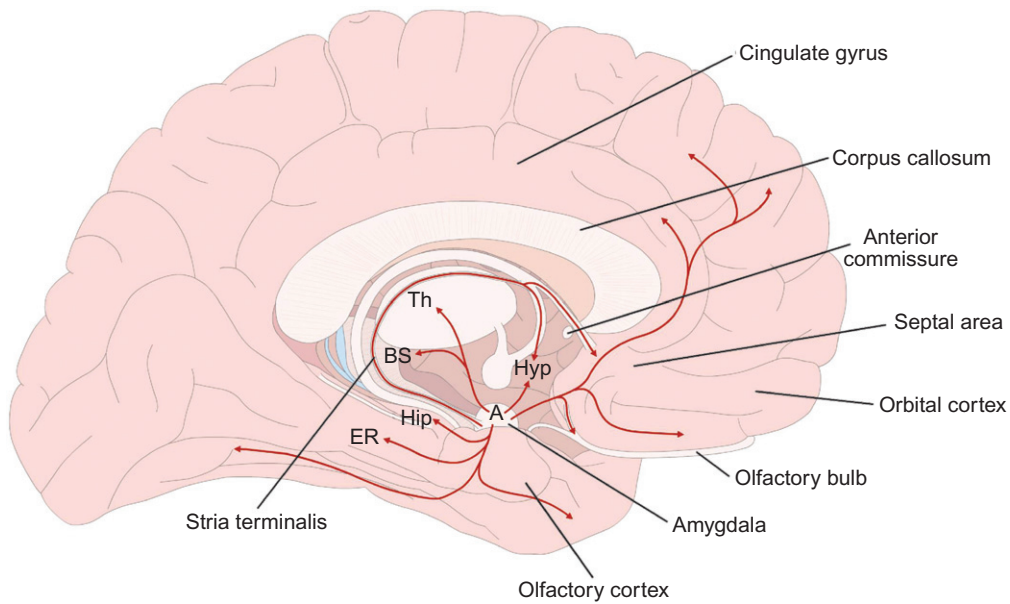


FIGURE 13.20 Efferent pathways from the amygdala. Hip 5 hippocampus; BS 5 brainstem; Th 5 thalamus; Hyp 5 hypothalamus; Am 5 amygdala.

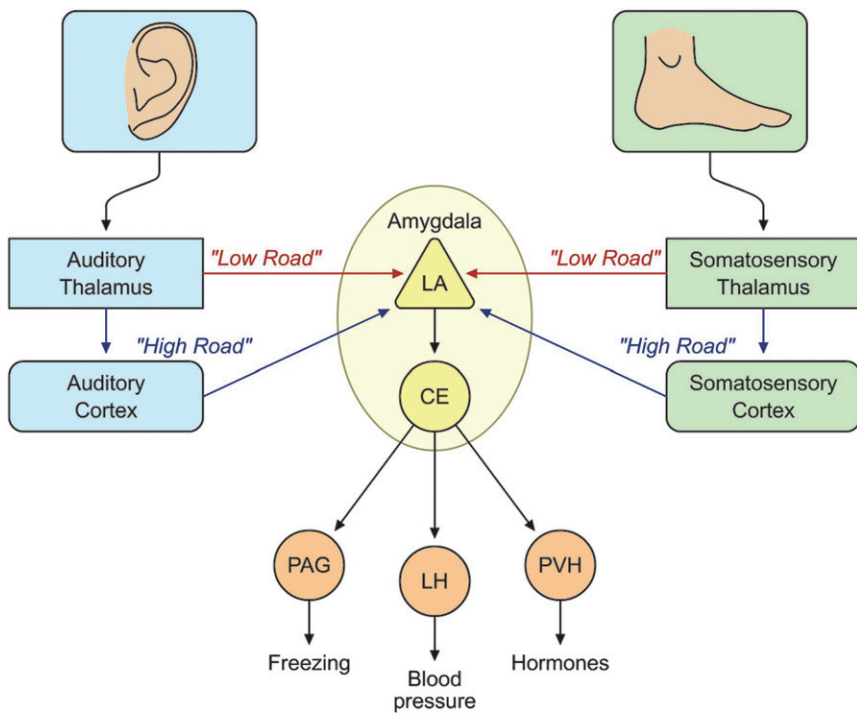


FIGURE 13.21 Two pathways to fear: the low road and the high road.

responding. The high road represents the pathway that is more influenced by social and personal decision-making processes and thus can reflect culture-specific emotional responses.

4.2 Faces and places: emotional perception in the brain

Does the addition of an emotional feeling change the way we perceive faces and places? In a study to address this question, Sabatinelli and colleagues (2011) looked at more than 150 neuroimaging studies of emotional face or scene processing. Figure 13.22 shows the results.

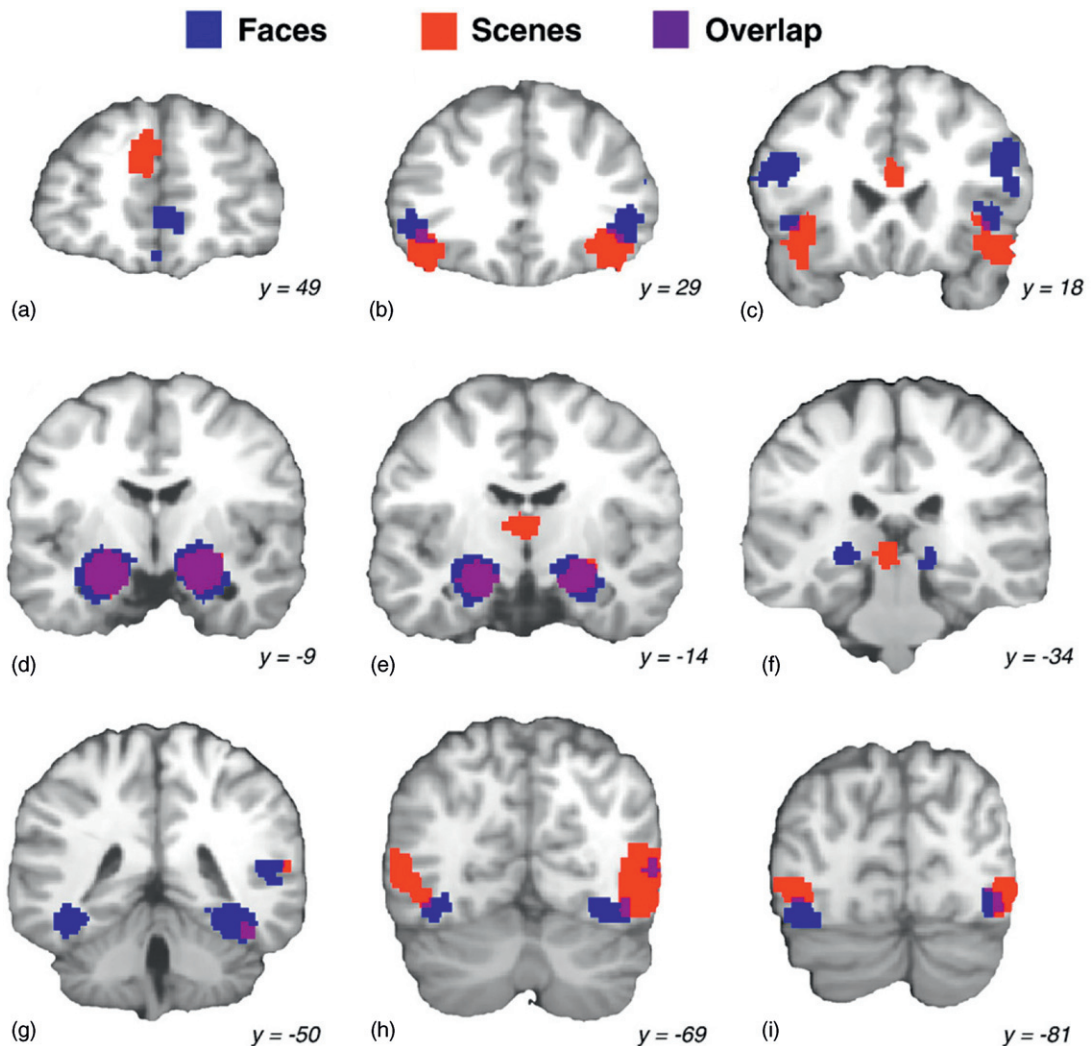
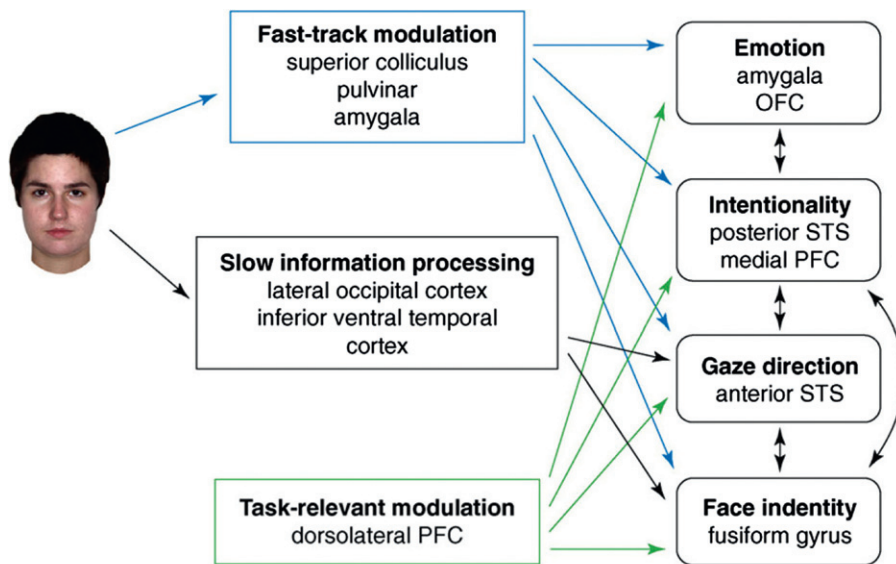


FIGURE 13.22 A meta-analysis of more than 150 neuroimaging studies of emotional face and scene processing showed differences for their perception. Face processing (in blue) and scene processing (in red) showed largely different brain activation patterns, although note the regions where they overlapped in the brain (in purple).

In general, the type of visual stimulus (face or scene) was processed in differing regions even when the emotional context was the same. For example, fearful faces and fearful scenes showed a differing pattern of brain response. Thus it is not simply the decoding of something *fearful* that is driving the brain response, but it is *what is fearful* (face or scene) that produces the difference in activation. While emotional faces and places were processed in large differing regions, note that some regions showed an overlap where both faces and places were processed (shown in purple).

4.2.1 A fast pathway for perceiving faces

Scientists have studied the effects of perceived eye contact on human behavior, called the “eye contact effect.” This is the phenomenon where perceived eye contact actually modulates areas in the social brain network, including both cortical and subcortical regions. One eye contact effect has been a “fast processing” effect when direct eye gaze is perceived. Why is the brain faster at processing this kind of stimulus? Eye gaze, as we have just discussed, is a very important social cue. It can be critical for survival if that gaze is menacing enough! To explain how this kind of stimulus gains a “faster” access to cortex, Senju and Johnson (2009) proposed a fast-track modulator model (Figure 13.23). This model includes a “fast pathway” for direct gaze perception using a subcortical route (blue lines) that interacts with other processes that are decoding important aspects of the eye gaze such as the social context.



TRENDS in Cognitive Sciences

FIGURE 13.23 The fast-track modulator model. Perceived eye contact (upper left) is initially detected by a subcortical route, which projects to various regions of the social behavior network (blue lines). This signal from the subcortical route then interacts with contextual modulation based on the task demands in addition to the social context (green lines) to modulate the response of these regions to the following input from a cortical route (black lines). Source: Senju & Johnson, 2009

4.3 Emotional memories

Psychological evidence has been available for some time indicating that moderate levels of emotional arousal (most often fear-based arousal) at the time of an event lead to better retention of explicit memories. For example, frightening films are better remembered than neutral films, with a linear relationship between degree of emotional arousal in the film (measured by self-report and by PET activity in the amygdala) and level of free recall (Cahill et al., 1996). The familiar inverted U-shaped function is in operation in predicting the interaction of emotion and memory consolidation. Too much activation in the amygdala leads to loss of explicit memories for emotional events (Cahill & McGaugh, 1998).

Pathways to consolidation of explicit memories seem to depend on reception of emotional stimuli by the amygdala, followed by activation of the hypothalamus and pituitary gland, resulting in release of the adrenomedullary hormone adrenaline and subsequently the adrenocortical hormone cortisol. Both adrenaline and cortisol (often called stress hormones) appear to influence the hippocampus-dependent formation of explicit memories (Figure 13.24). Improved memory for emotional stimuli is absent in patients with bilateral amygdala lesions (Cahill et al., 1995). The arousal effect due to stress hormone release can also be eliminated by

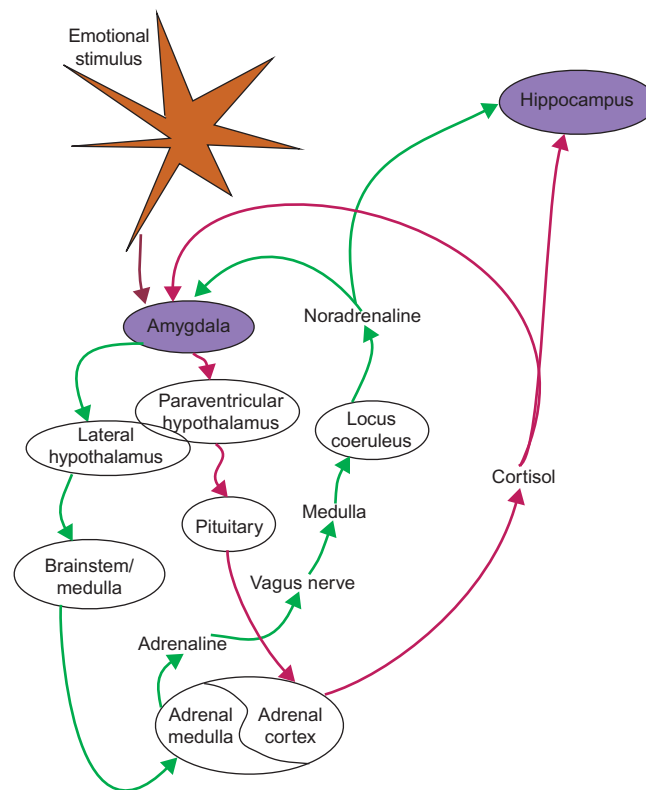


FIGURE 13.24 Stress hormones and explicit memory consolidation. Adrenaline pathway: green. Cortisol pathway: red. Notice that both pathways begin in the amygdala, circulate to the adrenal gland, and feed back to the amygdala and hippocampus after passing throughout the body.

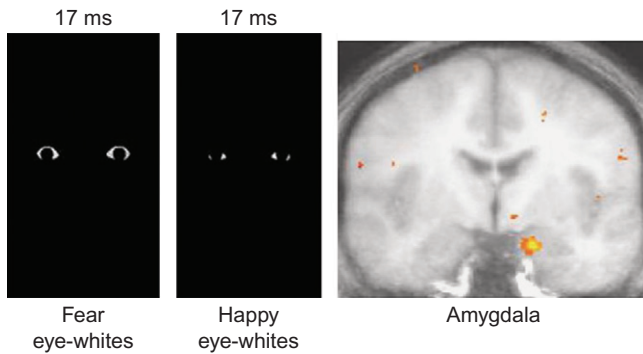


FIGURE 13.25 Amygdala responds to the whites of fearful eyes more strongly than to happy eyes. On the right, the BOLD response of the left ventral amygdala to fearful whites. Source: Whalen *et al.*, 2004, as adapted in Phelps & LeDoux, 2005.

administering Th-adrenergic antagonists (“beta blockers” such as propranolol) that block adrenaline receptors (Cahill *et al.*, 1994). These beta blockers act to help the natural adrenaline response caused by stress to occur, allowing patients with stress disorders to become calmed down. For example, posttraumatic stress disorders (PTSD) such as those experienced after serving in wars or by administration of propranolol in the emergency room soon after traumatic events (Pitman *et al.*, 2002).

4.3 Emotion and social behavior

Bilateral damage to the amygdala in monkeys causes dramatic changes in their behavior, including lack of fear for dangerous stimuli, eating inedible objects, and atypical sexual behavior (Kluver-Bucy syndrome). However, parallel behavioral changes have not been noted in human patients with lesions of the amygdala, presumably because humans have extensive neocortical social control and inhibition systems not available to other primates. There is, however, some evidence that more subtle deficits exist in patients with amygdala damage—for example, in processing of emotional facial expressions.

The amygdala responds to simple aspects of complex stimuli, specifically to low spatial frequency aspects of faces (Vuilleumier *et al.*, 2003). Consistent with this general rule, evidence shows that the amygdala responds to the wide-open eyes of fearful and surprised expressions. In a recent refinement, Whalen and his colleagues (Whalen *et al.*, 2004) found that the amygdala responded selectively to subliminally presented *whites* of fearful eyes compared to the whites of happy eyes (Figure 13.25).

Finally, Adolphs and colleagues (2005) found that patients with bilateral amygdala damage fail to look at the eyes when judging facial expression. This deficit may account for observed difficulties in interpretation of others’ emotions among such patients. Patients with amygdala lesions underestimate emotional intensity and overestimate trustworthiness and approachableness of others compared to nonlesioned participants.

5.0 CHAPTER REVIEW

The social brain has amazing abilities, from a “fast path” for recognizing faces to special circuits for recognizing emotions within those faces to detecting eye gaze and intent. Humans are excellent predictors in social situations, understanding other’s intentions, sharing their attention, and understanding what others know or feel. These abilities develop early in life

and are important stages of cognitive development. The advent of neuroimaging techniques has provided social cognition neuroscientists new ways to investigate the brain bases for these complex social abilities and processes. The brain areas for these social abilities are distributed throughout the cortex and into subcortical regions. Importantly, the social brain network is tightly coupled with the emotional pathways, providing the ability to decode not just a new face but the emotional expression on that face. Many open questions still remain to be discovered in the new field of social cognitive neuroscience, with new techniques being developed for uncovering the social brain's mysteries.

6.0 STUDY QUESTIONS

1. Briefly describe what is meant by a *theory of mind*.
2. According to Frith, what is mentalizing?
3. Why are shared attention mechanisms important for human development? When do they develop?
4. What role does context play in understanding intention?
5. What is the evidence that processing an emotion such as fearfulness may depend on what type of visual stimulus is fearful?

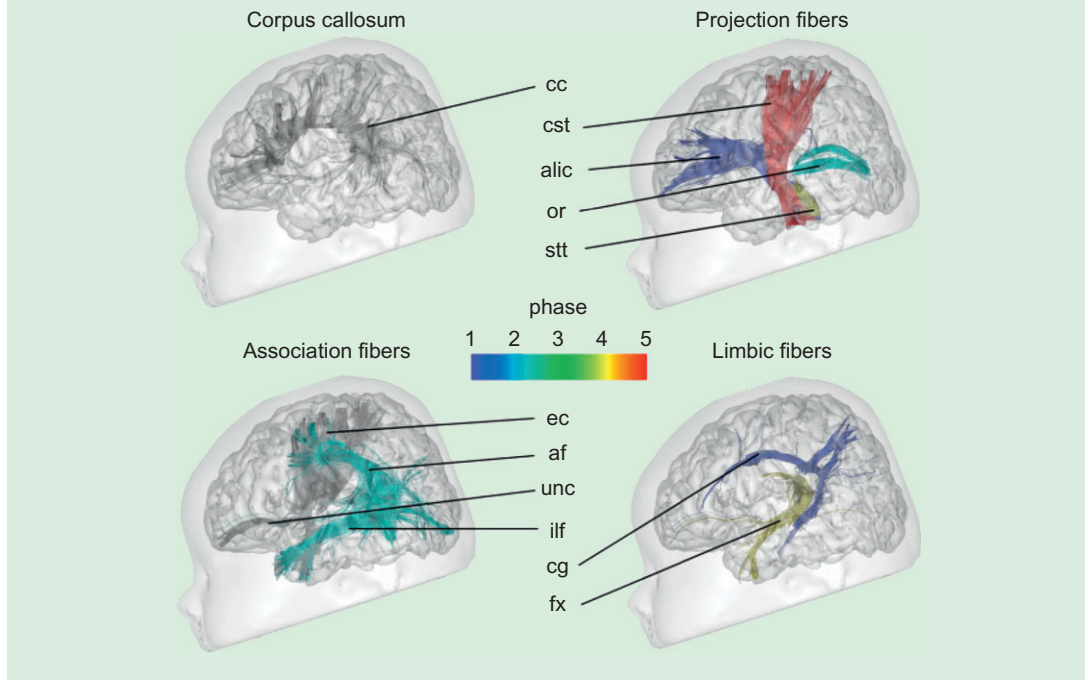
Growing up

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Life is a flame that is always burning itself out, but it catches fire again every time a child is born. **George Bernard Shaw**

The mature adult brain contains neural 'highways' that are well established and course throughout the brain. Until recently, little was known about the development of these neural highways in living infants. Using new diffusion tensor imaging techniques, the maturation of fiber bundles is studied in 1–4 month old infants. The color coding (from blue to red) shows the maturational phase of the fiber bundles. *Source: Dubois et al., 2009.*



1.0 INTRODUCTION

In this chapter, we provide an overview of how humans grow and develop across multiple stages of life: from prenatal to infancy, from child to adolescent. Much of our focus will be on early stages of brain and cognitive development because the first years of human life represent a dramatic explosion of neurodevelopmental change as babies learn about their world. We will explore the roles of nature and nurture in the development of the brain and mind, discovering the intricacies of the complex interactions between genetics and experience.

The field of developmental cognitive neuroscience is a relatively young one. The advent of new noninvasive ways to measure brain function in infants and children has literally revolutionized the study of what infants and young children understand about the world surrounding them. These techniques provide a safe way to look at brain changes and development during the early years of life when the brain is changing dynamically.

1.1 New techniques for investigating the developing brain

Two techniques that have been employed in studies of infants and young children are electroencephalography/event-related potentials (EEG/ERPs) and functional magnetic resonance imaging (fMRI) (Figure 14.1). While these techniques have revolutionized the

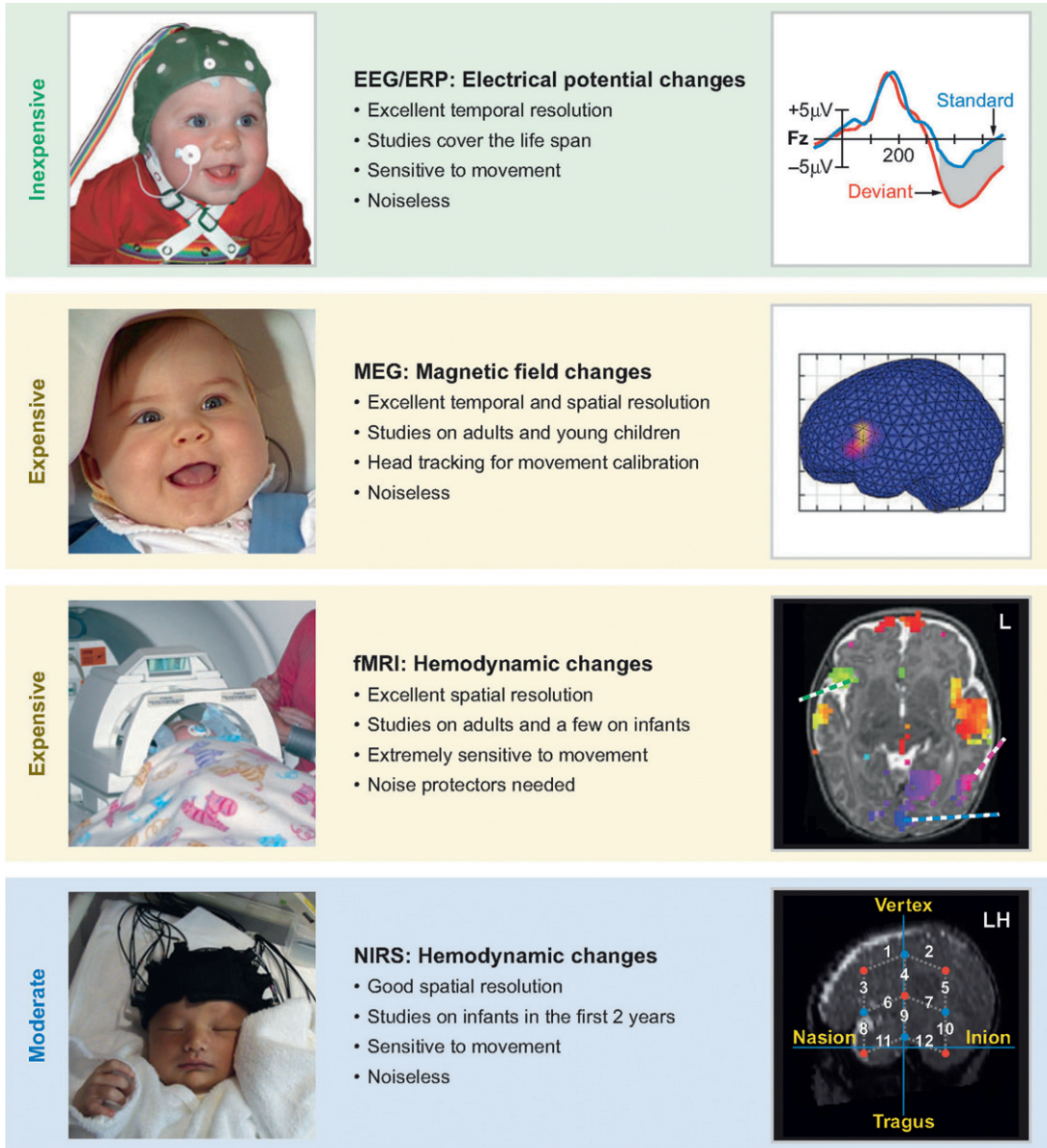


FIGURE 14.1 Shown are four neuroimaging techniques used with infants and young children. Top panel: EEG/ERP measures of electrical potentials. Second panel: MEG measures of magnetic fields. Third panel: fMRI measures of hemodynamic changes. Bottom panel: near-infrared spectroscopy (NIRS) measures of near-infrared light changes. Source: Kuhl & Rivera-Gaxiola, 2008, with permission.

field of cognitive neuroscience, nowhere is the effect felt as strongly as in the study of the unfolding of human brain development and its correspondence to behavior. Studies of adult behavior and brain function have informed us about how the typically developing brain functions across domains such as language, emotion, and memory. They also inform us about the effects of brain damage or disease. However, the pattern of deficit found in adults following brain damage differs sharply from the effects when brain damage occurs early in life. Therefore, the advent of neuroimaging techniques allows us to understand the brain regions and cognitive capabilities across cognitive domains while it is unfolding in development.

New and sophisticated methods to investigate anatomical developmental changes throughout life have also increased our ability to understand the complex patterns of brain development (Figure 14.2). These methods allow us to track the development of gray matter across brain regions, as well as to assess connectivity patterns across and between the cerebral hemispheres.

1.2 The mystery of the developing brain: old questions and new

In this chapter, we address some brain questions that have been asked for many years. A central question in human development is the trading roles of nature and nurture. A related issue is to what extent the brain is flexible in adapting to new situations in its environment and

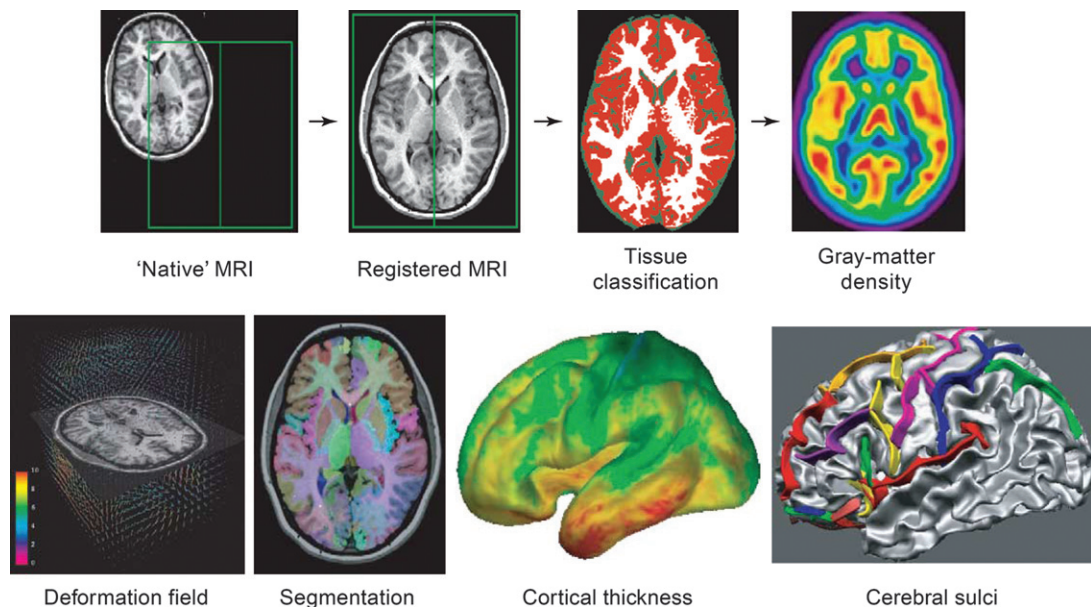


FIGURE 14.2 Image processing pipeline. *Top row:* A typical image processing pipeline begins with a transformation of a MRI image; this process generates an image that is “registered” with the template brain. The next step involves voxel-wise classification of brain tissue into gray matter (GM) (in red), white matter (in white), and cerebrospinal fluid (in green). Each image is filtered to generate “density” images (the “hotter” the color, from blue to red, the higher the GM density). *Bottom row:* By combining nonlinear registration with tissue classification, one can segment various brain structures, such as the frontal lobe or the amygdala. Other techniques produce maps of cortical thickness or identify sulci. Source: Paus, 2005.

to recover from damage. Some new questions can be posed that we were previously unable to address due to the limitation of our experimental approaches or techniques, such as what does a baby know before birth? What are the long-standing effects of very early brain damage? How do dynamic processes in brain development differ across brain regions and hemispheres? We will discuss advances in our knowledge about the developmental pathways of three main areas of cognition that have been a focus in the field: language, executive function, and social cognition.

2.0 PRENATAL DEVELOPMENT: FROM BLASTOCYST TO BABY

Much of this chapter is devoted to a discussion of brain development and its correspondence to cognition during infancy and childhood. Before we begin that discussion, we provide a brief description of the processes that occur before birth, during prenatal development. While little is known about the sensory, perceptual, or cognitive processes of a fetus in utero, recent investigations have focused on what a baby experiences before birth. These prebirth experiences can be critical for later development. And whether they are positive—hearing a mother’s voice or her heartbeat—or negative—experiencing the effects of maternal alcohol abuse—these prenatal experiences can have long-standing effects on later cognitive and social development. Let’s begin our prenatal section with a discussion on gene expression and the role of the environment.

2.1 Epigenesis

A central debate in the field of human development is the influence of nature versus nurture. Does our genetic makeup predetermine who we will become? Or does our experience shape who we are? Clearly, both genes and the environment have an impact on the developing human. Does gene expression unfold, followed by the development of brain structures and functions that later are affected by experience? Or does experience—the local environment, whether within a cell, a system, or the brain *in toto*—have an effect on gene expression? The interplay between genes and the environment is a complex one, with these interactive processes occurring long before birth. Here, we begin the topic of the cognitive neuroscience of human development with a discussion of the nature of epigenesis.

Epigenesis—the unfolding of genetic information within a specific context—is key to modern ideas about development. Different viewpoints on epigenesis underlie different perspectives on developmental cognitive neuroscience. Gottlieb and Halpern (2002) have drawn a useful distinction between “predetermined epigenesis” and “probabilistic epigenesis.” *Predetermined epigenesis* assumes that there is a unidirectional causal pathway from genes to brain anatomy to changes in the brain and cognitive function. A hypothetical example of this would be if the endogenous expression of a gene in the brain generated more of a certain neurochemical. Higher levels of this neurochemical might make a particular neural circuit active in the brain, and this additional neural activity allows for more complex computations than were previously possible. This increased cognitive ability will be evident in behavior as the child is able to pass a task that he or she failed at younger ages. In contrast, *probabilistic epigenesis* views the interactions among genes, structural brain changes, and

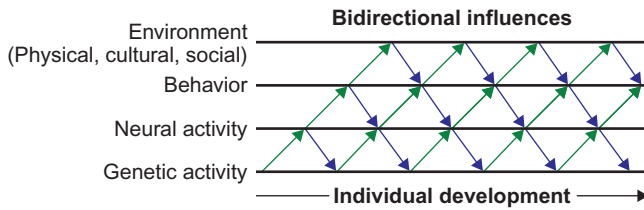


FIGURE 14.3 A systems view of psychobiological development. Source: Adapted from Gottlieb & Halpern, 2002.

function as bidirectional (Figure 14.3). Bidirectional interactions mean that not only can genes trigger a behavioral change but also that sensory input to the child can change patterns of gene expression. For example, we will hear later that newborn infants have primitive brain circuits that bias them to look toward the faces of other humans (Johnson, 1991). This early attention to faces results in some of the neural circuits involved in the visual pathways of the baby becoming shaped or tuned to process faces. The neuroanatomical changes that underlie this shaping process are due to differential gene expression.

2.2 The anatomy of brain development

Much of early brain development occurs in the first weeks following fertilization. Shortly after conception, a fertilized cell undergoes a rapid process of cell division, resulting in a cluster of proliferating cells (called the *blastocyst*) that resembles a tiny bunch of grapes (Figure 14.4). After a few days, the blastocyst differentiates into a three-layered structure (the embryonic disk). Each of these layers will subsequently differentiate into a major organic system, with the *endoderm* (inner layer) becoming internal organs (digestive, respiratory, etc.), the *mesoderm* (middle layer) becoming skeletal and muscular structures, and the *ectoderm* (outer layer) developing into the skin surface and the nervous system (including the perceptual organs).

The nervous system itself begins with a process known as *neurulation*. A portion of the ectoderm begins to fold in on itself to form a hollow cylinder called the *neural tube* (Figure 14.5). The neural tube differentiates along three dimensions: length, circumference, and radius. The length dimension differentiates into components of the central nervous system, with the fore-brain and midbrain arising at one end and the spinal cord at the other. The end of the tube that will become the spinal cord differentiates into a series of repeated units or segments, while the other end of the neural tube organizes and forms a series of bulges and convolutions. Five weeks after conception, these bulges become protoforms for parts of the brain. One bulge gives rise to the cortex, a second becomes the thalamus and hypothalamus, a third turns into the midbrain, and others form the cerebellum and medulla.

The distinction between sensory and motor systems develops along the axis tangential to the surface of the neural tube with the dorsal (top side) becoming mainly sensory cortex, and the ventral (bottom side) developing into motor cortex. The various association cortices and “higher” sensory and motor cortices tend to arise from the tissue between.

2.3 Neural migration

Most cortical neurons in humans are generated outside the cortex itself in a region just underneath what becomes the cortex: the “proliferative zone.” After young neurons are born, they have to *migrate* from the proliferative zone to the particular region where they will

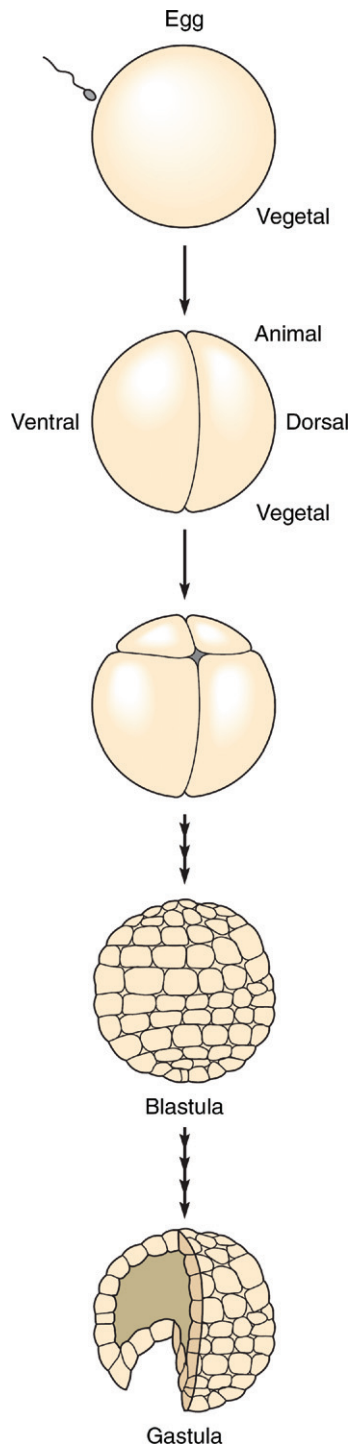


FIGURE 14.4 Blastocyst development. The early processes of animal development follow a conserved pattern; after fertilization, a series of cleavage divisions divide the egg into a multicellular blastula. The process of gastrulation brings some of the cells from the surface of the embryo to the inside and generates the three-layered structure common to most multicellular animals. Source: *Sanes et al., 2006*.

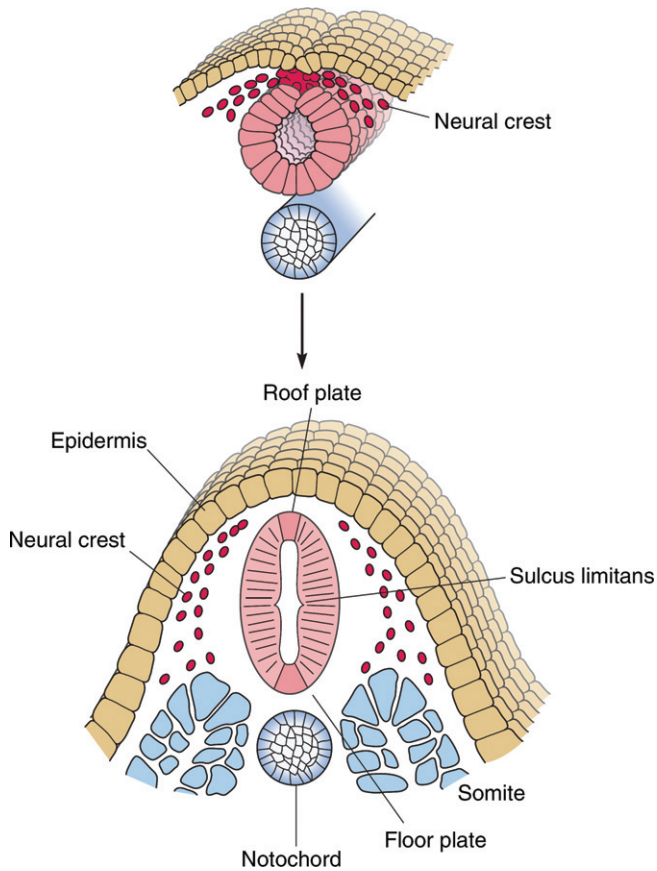


FIGURE 14.5 The neural tube. The overall organization of the neural tube emerges soon after closure. The most ventral (lowest) part of the neural tube becomes flattened into a distinct “floor plate.” The most dorsal (highest) aspect develops into a tissue known as the roof plate. Source: *Sanes et al., 2006*.

be employed in the mature brain. The most common type of migration involves *passive cell displacement*. In this case young cells are simply pushed farther away from the proliferative zone by more recently born cells. This gives rise to an outside-to-inside pattern, resulting in the oldest cells ending up toward the surface of the brain, while the youngest cells are toward the inside. This type of migration gives rise to brain structures such as the thalamus and many regions of the brainstem.

The second form of migration is more active and involves the young cell moving past previously generated cells to create an “inside-out” pattern. This pattern is found in the cerebral cortex and in some subcortical areas that have a laminar structure (divided into parallel layers).

The best-studied example of active migration comes from the prenatal development of cerebral cortex and the *radial unit model* proposed by Pasko Rakic (1988). According to his model, the laminar organization of the cerebral cortex is determined by the fact that each

relevant proliferative unit gives rise to about 100 neurons. A radial glial fiber is a long process that stretches from top to bottom of the cortex and originates from a glial cell. Radial glial fibers effectively act like a climbing rope to ensure that neurons produced by one proliferative unit all contribute to one radial column within the cortex. The progeny (“children”) from each of the proliferative units all migrate up the same radial glial fiber, with the latest to be born traveling past their older relatives (Figure 14.6).

Thus, in the early weeks of gestation, the embryo undergoes complex processes that form the basis for the central nervous system. It is important to note that prenatal brain development is not a passive process involving the unfolding of genetic instructions. Rather, from an early stage *interactions* between cells are critical, including the transmission of electrical signals between neurons. Thus, waves of firing intrinsic to the developing organism may play an

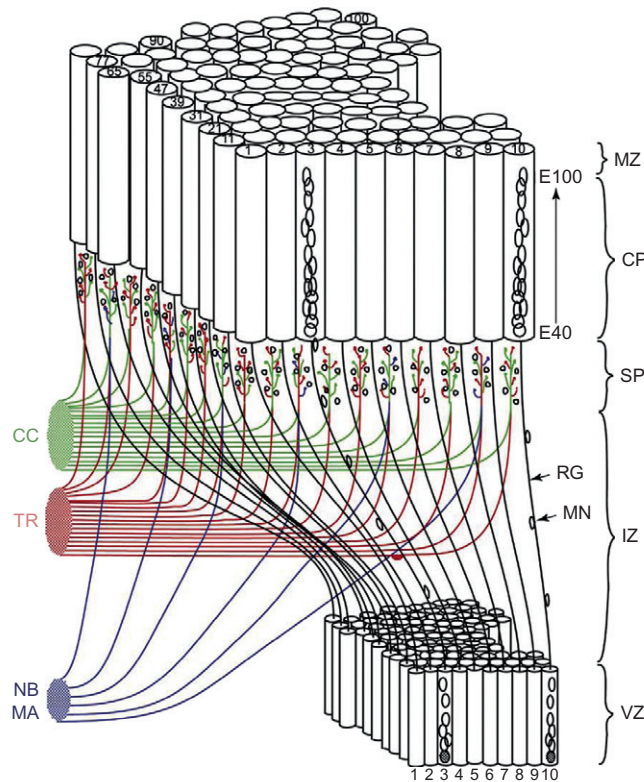


FIGURE 14.6 The radial unit model of Rakic (1988). Note how the radial glial fibers extend from the ventricular zone (VZ, bottom) to the cortical plate (CP) via a number of regions: the intermediate zone (IZ) and the subplate zone (SP). RG indicates a radial glial fiber and MN a migrating neuron. Each MN traverses the IZ and SP zones that contain waiting terminals from the thalamic radiation (TR) and cortico-cortico afferents (CC). After entering the cortical plate, the neurons migrate past their predecessors to the marginal zone (MZ). Source: Rakic, 2009.

important role in specifying aspects of brain structure long before sensory inputs from the external world have any effect.

2.4 Nature and nurture revisited

The role of the prenatal environment in brain development can have long-lasting effects, both good and bad. The developing infant is susceptible to events occurring within this environment. One such event is the incursion of a *teratogen*. A teratogen is defined as any environmental agent that causes damage during the prenatal period. Examples of teratogens are prescription and even nonprescription drugs, caffeine found in coffee and soft drinks, illegal drugs such as cocaine and heroin, tobacco and marijuana products, and alcohol. The effects of the teratogen(s) can be complex depending on the dosage level, the time it occurs during prenatal development, and the genetic makeup of the mother, since some individuals are more susceptible than others.

The prenatal brain is particularly susceptible to the effects of alcohol. Alcohol abuse by the mother during pregnancy results in long-term deficits in cognition, language, and social development called *fetal alcohol syndrome* (FAS) (Jones & Smith, 1973). A recent brain mapping study of children, teenagers, and young adults with severe FAS showed gray matter density differences in FAS individuals as compared to age- and gender-matched controls. Specific findings were reduced gray matter density in frontal and parietal areas and increased density in temporal and inferior parietal lobe regions (Figure 14.7). These brain areas mature throughout childhood and into late adolescence; therefore, these gray matter density differences in FAS individuals indicate that prenatal exposure to alcohol has a resounding and long-lasting impact on brain development and cognitive development throughout the lifespan.

Longitudinal studies assessing the long-term effects of smoking cigarettes or marijuana during pregnancy have provided new evidence about their impact on a child's cognitive

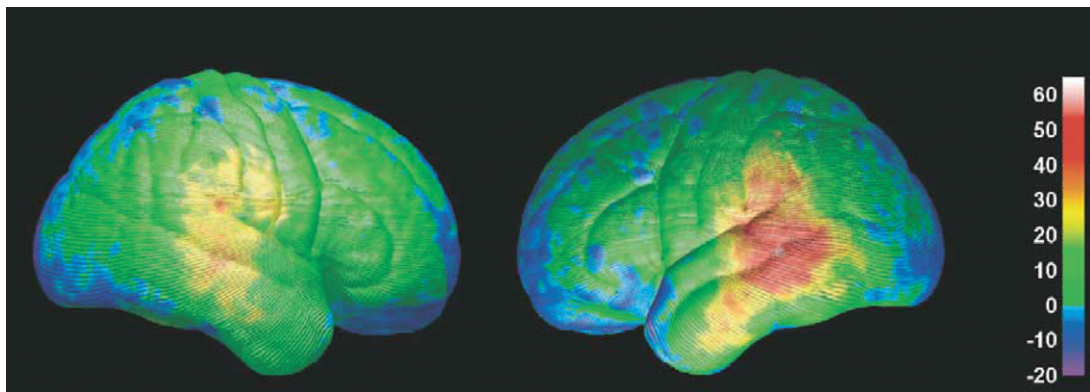


FIGURE 14.7 Differences in gray matter density between children with fetal alcohol syndrome (FAS) and typically developing controls. Warm (red, yellow) colors represent positive differences, indicating an increase in gray matter density (and thus a decrease in normal “pruning”) in those regions as compared to controls. Note that the children with FAS have much increased densities in temporal lobe regions, particularly in the left hemisphere. (Adapted, with permission, from Sowell et al., 2002.) Source: Toga et al., 2006.

development. Fried and colleagues (2003) have followed a cohort of children in Canada from birth through young adulthood. Using neuropsychological test batteries to assess cognitive functions like verbal intelligence, visuospatial processing, language abilities, and attentional function, Fried and colleagues found that there are early-occurring (by age 3) and long-lasting cognitive impairments caused by the mother smoking either tobacco or marijuana during pregnancy. The specific effects of prenatal exposure to cigarette smoke differ sharply from exposure to marijuana, although both cause harm. Exposure to cigarette smoke resulted in lower general intelligence in the children, coupled with deficits in auditory function and verbal working memory that continued from early childhood (age 3) through adolescence (age 16) (Fried et al., 2003). Exposure to marijuana smoke resulted in no general intelligence deficit; however, executive functions, such as attention and working memory, were impaired in these children and, in particular, visual processes such as visual integration, analysis, and reasoning. Again, these impairments were observed early (age 3) and continued through the teenage years.

The cognitive impairments reflected by the neuropsychological test batteries implicated specific brain regions for further study of the effects of prenatal exposure to cigarette and marijuana smoke. Visuospatial integrative processes tap frontal lobe regions in adults. Fried and colleagues (Smith et al., 2006) continued their investigation into the long-term effects of prenatal exposure to marijuana using a neuroimaging technique, fMRI, with a sample of young adults (18–22 years) from the Canadian cohort with prenatal exposure to marijuana smoke. Results of the study revealed a differing pattern of neural activity in frontal lobe regions that are engaged in a visuospatial task. Specific findings were reduced activity in right hemisphere regions (Figure 14.8, upper panel) and increased activity in left hemisphere regions (Figure 14.8, lower

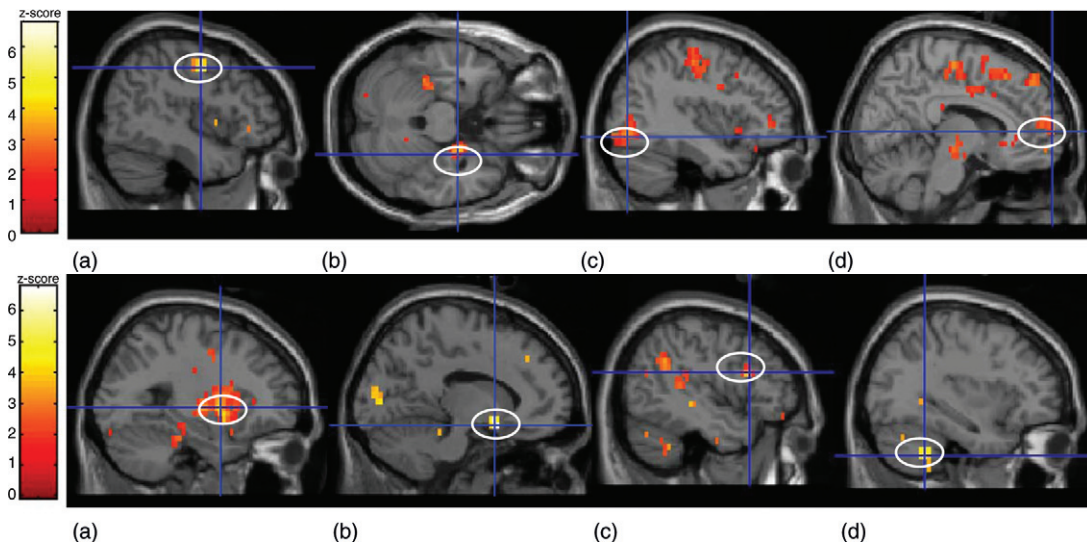


FIGURE 14.8 Effects of prenatal use of marijuana smoke on young adults (18–22 years) measured using fMRI. Frontal lobe circuits engaged in a task tapping visuospatial working memory systems, with reduced right hemisphere activity (upper panel) and increased left hemisphere activity (lower panel) as compared to an age-matched control group. Source: *Smith et al., 2006*.

panel). The authors interpreted these findings as indicating that right hemisphere neural circuitry engaged in tasks that tap visuospatial short-term memory are less active in children with prenatal marijuana smoke exposure. While it is difficult to know at this stage of the research just why left hemisphere activity was increased, it could be that left hemisphere regions were recruited as a compensatory mechanism due to the decreased neural activation in the right hemisphere. The work of Fried and colleagues provide compelling evidence that the damage appears early in a child's cognitive development and is very long lasting.

2.5 Prenatal hearing experience: voice and music perception before birth

What do babies know before they are born? Is it important for a mother-to-be to talk to her unborn baby? Read to her baby? Sing to her baby? Is there an impact on later language, music, and cognitive function? In other words, what are the perceptual abilities of an unborn child, and how do they relate to later cognitive development? This question has intrigued developmental psychologists for at least a hundred years (see Kisilevsky & Low, 1998, for a review), but systematic investigations of fetal perception did not get under way until the 1980s. How do you measure a fetal response to sounds? Usually, the investigators measure heart rate changes and sometimes body movements in response to differing types of sounds. These early studies provided evidence that by approximately 30 weeks' gestational age, a fetus hears and responds to simple sounds such as bursts of white noise. By 37–42 weeks, a fetus can discriminate between types of speech sounds (such as vowels, consonant-vowel syllables) (Lecanuet et al., 1987; Groome et al., 1999).

The finding that a fetus can both hear and discriminate between sounds before birth has led to investigations of what a fetus knows about specific sounds—namely, his or her own mother's voice. DeCasper and colleagues studied the listening preferences of newborn infants in a series of investigations in the 1980s. They found that newborns prefer their mother's voice to that of a female stranger (DeCasper & Fifer, 1980). A more recent study used event-related potentials (ERPs) to compare brain responses in newborn (less than 1 day old) infants to presentations of their mother's voice versus a stranger's voice (Beauchemin et al., 2011). Results showed different brain patterns for the mother's voice, which activated left hemisphere language regions, as compared to the stranger's voice, which activated right hemisphere voice processing regions (Figure 14.9). As early as 100 ms (1/10th of a second) after the voice sounds are presented, newborns show a left hemisphere response for their mother's voice and a differing response—in the right hemisphere—when the voice is of a stranger. These findings provide evidence that a mother's voice is preferentially processed, even immediately after birth, reflecting prenatal experience with the mother's voice.

3.0 THE DEVELOPING BRAIN: A LIFETIME OF CHANGE

3.1 The rise and fall of postnatal brain development

While the overall appearance of the newborn human brain is rather similar to that in adults, and most neurons have already reached their final locations, a number of substantive *additive* changes occur during postnatal development of the brain. Specifically, brain volume

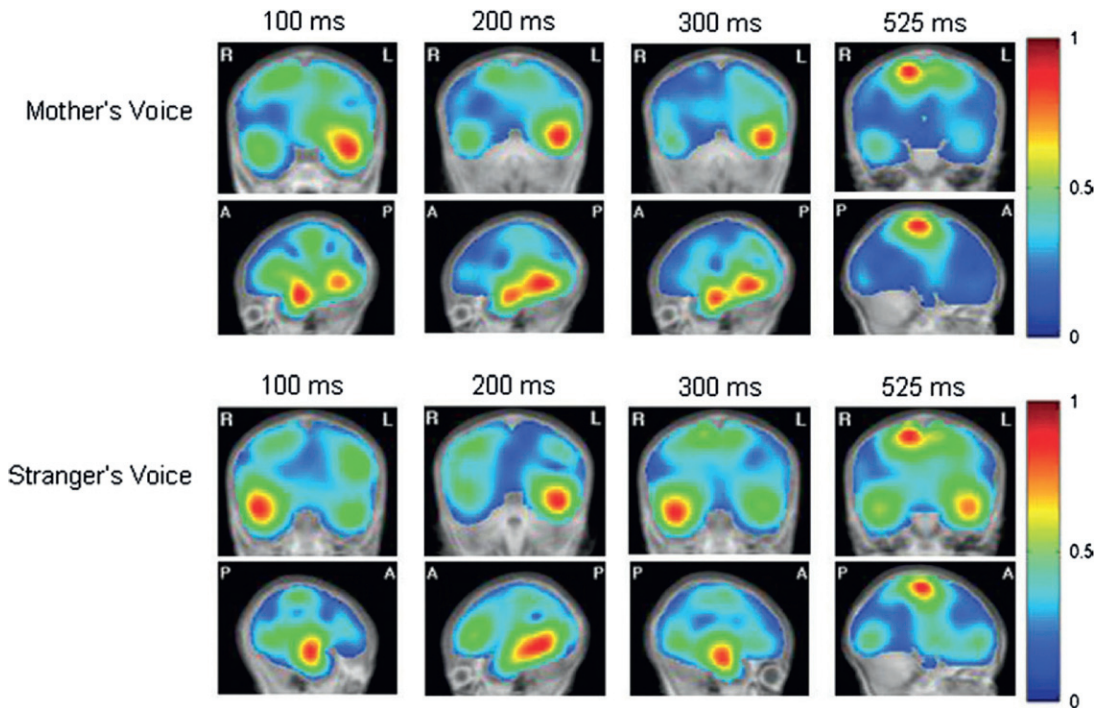


FIGURE 14.9 Brain responses from newborn infants for their mother's voice (top panels) and a stranger's voice (lower panel). Note that as early as 100 ms (1/10th of a second) after the voice sounds are presented, newborns show a left hemisphere response for their mother's voice and a different response—in the right hemisphere—when the voice is of a stranger. These findings provide evidence that a mother's voice is preferentially processed, even immediately after birth, reflecting prenatal experience with the mother's voice.

quadruples between birth and adulthood, an increase that comes from a number of sources, but generally not from additional neurons. The generation and migration of neurons takes place almost entirely within the period of prenatal development in the human.

Perhaps the most obvious change during postnatal neural development is the increase in size and complexity of the *dendritic trees* of most neurons. An example of the dramatic increase in dendritic tree extent during human postnatal development is shown in [Figure 14.10](#). While the extent and reach of a cell's dendritic arbor may increase dramatically, it also often becomes more specific and specialized.

In addition to the more extensive processes involved in the inputs and outputs of cells, there is a steady increase in the density of synapses in most regions of the cerebral cortex in humans (Huttenlocher et al., 1982; Huttenlocher, 1990, 1994). The process of creating new synapses, *synaptogenesis*, begins approximately around the time of birth for all cortical areas studied to date, with the most increases, and the final peak density, occurring at different ages in different areas. For example, in the visual cortex there is rapid synaptogenesis at 3 to 4 months, and the maximum density of around 150 percent of that seen in adult humans is reached between 4 and 12 months.

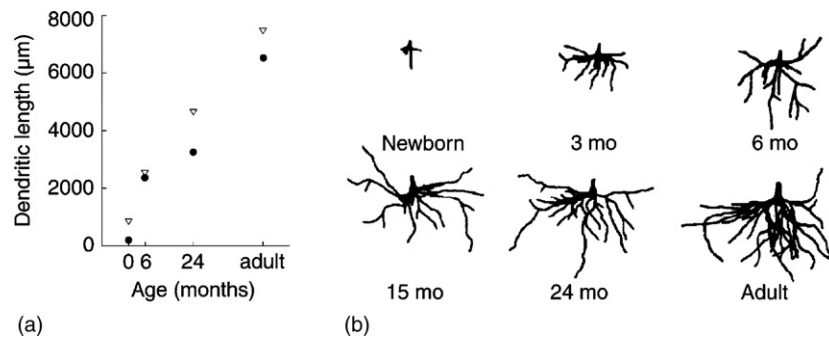


FIGURE 14.10 Dendritic arborization. A drawing of the cellular structure of the human visual cortex based on Golgi stain preparations from Conel (1939–1967). Source: Quartz, 1999, from Conel, 1953.

Another additive process is *myelination*. Myelination refers to an increase in the fatty sheath surrounding neuronal processes and fibers that increases the efficiency of electrical transmission. This sheath is white, so myelinated fibers are referred to as *white matter*. Changes in the extent of white matter are of interest, since they presumably reflect interregional communication in the developing brain. While increases in white matter extend through adolescence into adulthood, particularly in frontal brain regions (Huttenlocher et al., 1982), the most rapid changes occur during the first 2 years. Myelination appears to begin at birth in the pons and cerebellar peduncles and, by 3 months, has extended to the optic radiation and splenium of the corpus callosum. Around 8–12 months the white matter associated with the frontal, parietal, and occipital lobes becomes apparent (Figure 14.11).

Surprisingly, human postnatal brain development also involves some significant *regressive events*. One quantitative neuroanatomical measure of a regressive event is the density of synapses, where there is a period of synaptic loss or *pruning* (Huttenlocher, 1990, 1994). Like the timing of bursts of synaptogenesis, and the subsequent peaks of density, the timing of the reduction in synaptic density appears to vary between cortical regions, at least in humans. For example, synaptic density in the visual cortex begins to return to adult levels after about 2 years, while the same point is not reached until adolescence for regions of the prefrontal cortex. Huttenlocher (1990, 1994) suggests that this initial overproduction of synapses may have an important role in the apparent plasticity of the young brain.

Thus, the *rise and fall* developmental sequence is seen in a number of different measures of neuroanatomical and physiological development in the human cortex. However, we need to bear in mind that not all measures show this pattern (e.g., myelination) and that measures of synaptic density are static snapshots of a dynamic process in which both additive and regressive processes are continually in progress.

3.2 Regional differences in brain development

As compared to other species, humans take a very long time to develop into independent creatures. Human postnatal cortical development, for example, is extended roughly four times as long as nonhuman primates. The “down” side of this slow development is that there are many years during which a child is highly dependent on the care provided by family

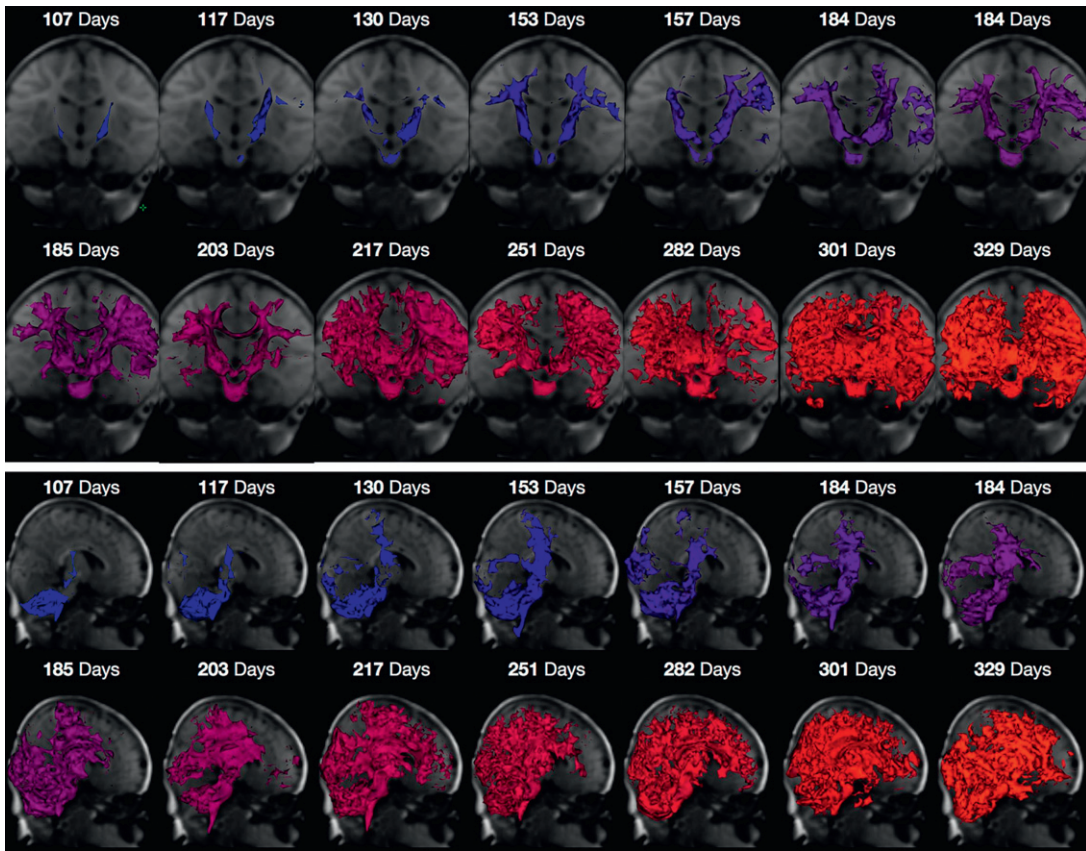


FIGURE 14.11 Myelin maturation in infants. Top panel shows a coronal slice and bottom panel shows a sagittal slice. The age of the infant is shown in days above the images. Note the rapid development of myelination during the first months of life (107 days, blue) to approximately 1 year (329 days, red).

members. The “up” side of this protracted developmental timetable is that the human brain has far more opportunity for experience, and interactions with others, to shape and mold its development.

The rise and fall pattern of additive and regressive events occurs at different time frames in regions and lobes in the human brain. These events are heavily experience driven and reflect synapse formation and dendritic arborization that are due to cognitive and sensory development, learning, and integrative processes that occur throughout infancy and childhood and continue through the teen years. A time course of brain development from conception to late teens is presented in [Figure 14.12](#) (Casey et al., 2005). Prenatal changes are shown on the left side of the figure and largely reflect neurulation, cell proliferation, and migration processes. Postnatal changes reflect developmental processes such as synaptogenesis and dendritic arborization. Sensory areas for processing visual and auditory information, for example, develop earlier than frontal lobe regions such as the prefrontal cortex for processing executive functions (Casey et al., 2005).

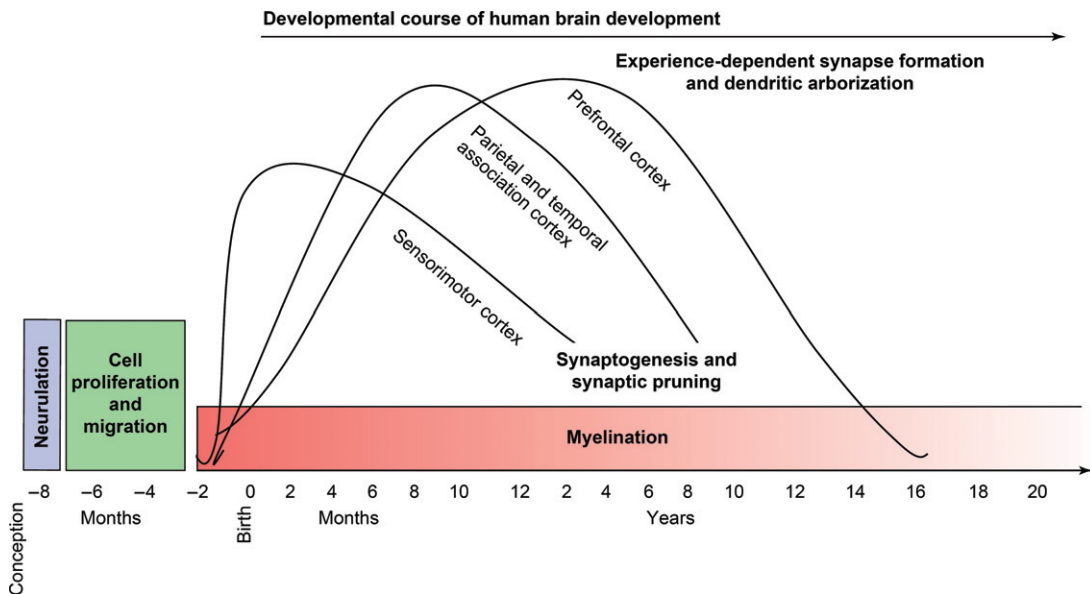


FIGURE 14.12 The human brain undergoes dramatic changes in both its structural architecture and functional organization that reflect a dynamic interplay of simultaneously occurring progressive and regressive events. Although the total brain size is about 90 percent of adult size by age 6 years, the brain continues to undergo dynamic changes throughout adolescence and well into adulthood. This figure illustrates some of these developmental changes, including proliferation and migration of cells mostly during fetal development, regional changes in synaptic density during postnatal development, and protracted development well into adulthood. (Adapted from Thompson & Nelson, 2001.) Source: Casey *et al.*, 2005.

While we are beginning to map out the developmental patterns for brain regions across the lifespan, a key issue that is being addressed is the notion of individual differences in how the brain matures and the correspondence to cognitive development. In other words, what is the relationship between brain and behavior? Do differing patterns of brain development reflect different levels of intellectual ability? These questions were addressed in a recent neuroimaging investigation of gray matter density in a large sample of more than 300 children and adolescents (Shaw *et al.*, 2006). The sample was a priori divided into three groups based on their performance on an IQ battery of tests: “Superior” with IQ ranging from 121 to 149; “High” with IQ ranging from 109 to 120; and “Average” with IQ ranging from 83 to 108. The results indicated that there are, indeed, differing patterns of brain change corresponding to overall level of intelligence (Figure 14.13). The notable finding was that high IQ was associated with thinner cortex, especially in frontal and temporal lobe areas, in early childhood. By late childhood, the opposite pattern was found, with high IQ associated with thicker cortex.

The important finding of this study was that there was a differing pattern of cortical development in frontal lobe regions for children in the “Superior” group as compared to either of the other groups. Specifically, there were differences in the dynamic rate of cortical thickening and thinning throughout early childhood and into adolescence and early adulthood. The authors concluded that differences in gray matter density in and of itself did

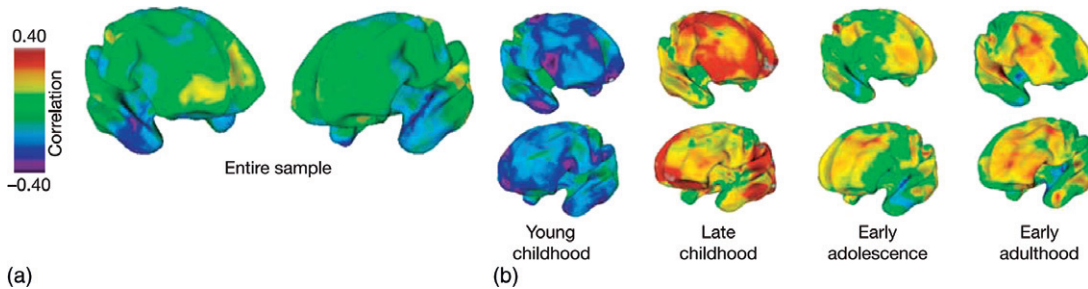


FIGURE 14.13 Correlations between IQ and cortical thickness. (a) correlations for all 307 subjects were generally positive and modest ($p < 0.05$), with r between 0 and 0.10 (green/yellow), except in the anterior temporal cortex (which showed a negative correlation, with r between 0 and 0.21; blue/purple). (b) Correlations in different age groups showed that negative correlations were present in the youngest group, indicating that higher IQ was associated with a thinner cortex, particularly in frontal and temporal regions. The relationship reverses in late childhood, with most of the cerebral cortex correlating positively with IQ. Source: *Shaw et al., 2006*.

not lead to children with superior intellectual abilities; rather they suggested that the dynamic properties of development of the cortex corresponded to level of intelligence, perhaps enabling the child to extract more information from his environment. Questions have been raised by this study: Are dynamic changes in brain growth patterns due to genetic predispositions in the “Superior” group? Or do they reflect differences in the environment? Or do they reflect a combination of both genetic influences and experience?

These findings from recent studies of brain development are helping us to prepare new models for human cognitive growth and the correspondence to cognition. These studies are still very early work in an ongoing series of investigations of complex brain developmental processes.

4.0 DEVELOPING MIND AND BRAIN

We have seen that the brain undergoes significant developmental changes throughout childhood. An important question to address in the field of developmental cognitive neuroscience is how these brain changes reflect development of cognitive processes. New techniques are allowing us to begin to map brain development and the correspondence to cognition.

Once again, the question of the role of nature versus nurture is debated in the field. Is the human brain prewired for language? Face perception? Or are these processes based on experience throughout life? Since these topics are of central interest in the study of human development, we will focus on three general areas of developmental cognitive neuroscience: the emergence of language; the development of cognitive control mechanisms; and the development of social cognition, with a specific focus on face perception. In the following section, we provide a brief summary of research to date on these topics in infants during the first year of life. Next, we present findings on these topics for older children and adolescents. Last, we review the effects of early (perinatal) brain damage on these systems.

4.1 The first year of life: an explosion of growth and development

The human brain increases fourfold in size from newborn to adult. Many of the dynamic changes that occur in development happen during the first year of life. During this 12-month span, an infant develops from a tiny creature with few voluntary movements to a busy toddler smiling, reaching for attractive objects, producing many speech sounds, crawling, and even walking as he or she explores the world.

4.1.1 *Developing the language brain: infant language capabilities*

Remember the studies showing that babies can hear and discriminate their mother's voice before birth? Studies like these have provided compelling evidence that a newborn infant already has experience with human language. We have discussed the nature versus nurture debate regarding the genetic predisposition for language versus the role of experience. This debate has been influential in the field of developmental cognitive neuroscience, with many studies investigating just what an infant knows about language. Most studies of young infants (less than 12 months old) focus on the classes and categories of speech sounds: phonology. Studies with older infants and children also investigate semantic (meaning-based) and syntactic (grammar-based) knowledge.

Is language "biologically special"? One way to address this question is to see whether young babies are specifically sensitive to human speech. If there are specific neural correlates of speech processing observable very early in life, this may indicate language-related neural processing prior to significant experience. Dehaene-Lambertz and her colleagues (2006) conducted a series of studies investigating this. One finding is that there are hemisphere differences for language processing that are emerging in infants as young as 3 months (Figure 14.14). Although work with adults has shown increasing evidence for speech processing in both left and right temporal lobes (Hickok & Poeppel, 2007), these data from the lab of Dehaene-Lambertz show a left-lateralized response in infancy.

Intriguingly, and unlike adults, human infants can initially discriminate a very wide range of phonetic constructs, including those not found in their native language (Eimas et al., 1971). For example, Japanese infants, but not Japanese adults, can discriminate between "r" and "l" sounds. However, this ability becomes restricted to the phonetic constructs found in their native language by around 10 months of age. These findings might reflect early speech perceptual processes that take into account the physical or acoustic features in all speech sounds in early infancy, developing later into mechanisms with less reliance on the physical aspects and more on the *abstract representations* of phonemes in their native language. In this way, the role of experience has a strong hand in shaping an infant's language knowledge.

How do infants "break" the speech code? How do they learn to separate the continuous speech sounds into words? Phrases? Sentences? Dr. Jenny Saffran has investigated how infants learn language for several years, and her research has provided groundbreaking new strides in understanding this complex learning phenomenon. Dr. Saffran theorizes that one important aspect of infant language learning is that infants unconsciously extract statistical regularities in the speech stream (Saffran et al., 1997). Here is how she proposes it happens: Within any given language, there are sound patterns that occur with some level of probability. Although all languages have many individual phonemes (sounds that are specific to that language), they form a finite set. And the way they are combined to form words is

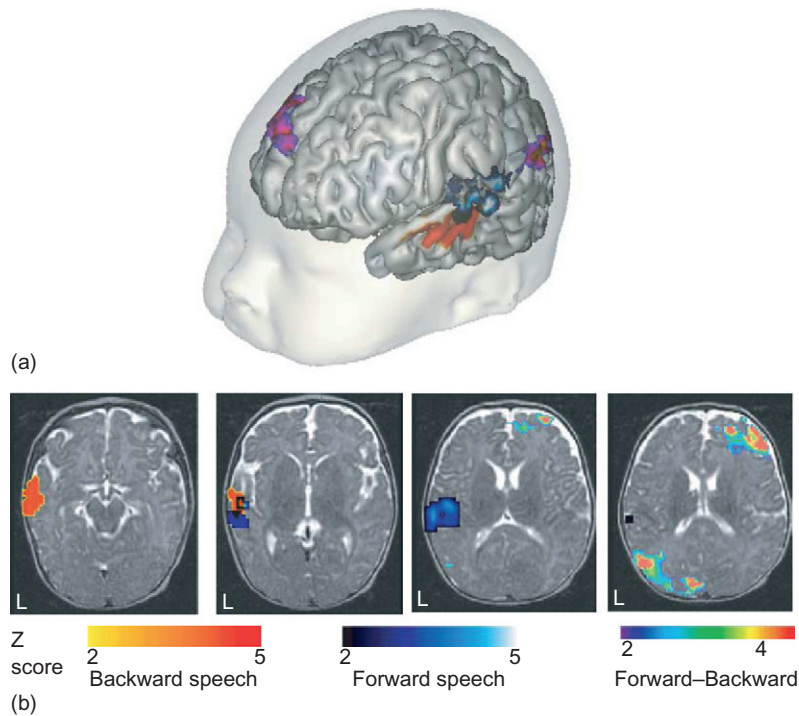


FIGURE 14.14 As early as 3 months, infants show a leftward laterality for human speech. Moving from left to right, the brain figures reflect (i) brain activation in the temporal lobe for backward speech (orange); (ii) brain response in a slightly higher brain slice, showing activation for both backward speech and forward speech (blue); (iii) brain response in a slightly higher brain slice showing activation for forward speech; (iv) the differing in brain activation for forward-backward speech shows activation in right prefrontal cortex. Source: *Dehaene-Lambertz et al., 2006*.

also constrained; it is not an infinite number of variations. Dr. Saffran theorizes that infants extract (learn) the transitional probability (TP) of sound patterns in speech. That is, the probability that a certain sound pattern will follow any given sound pattern, conditioned on the probability of the first sound pattern.

Sound complicated? Here is an example: In English, the syllable “ba” is very frequently followed by the syllable “by” to form the word “baby”—and this is a word that an infant hears a lot! This TP of the syllable “by” following “ba” is much higher than, say, “sin” to form the word “basin.” According to Dr. Saffran, infants extract these probabilities and learn to form word boundaries using these statistical learning mechanisms. Dr. Saffran has recently expanded her research to investigate how infants learn “rules” about their world in other domains besides language. Using pictures of dogs of different breeds that are presented in a learned pattern (ABA, ABB) or a new one, she and her colleagues have provided evidence that infants of 7 months use similar learning processes in decoding linguistic and nonlinguistic information (Figure 14.15).

How does infant language learning affect the brain? And how does brain development affect language learning? Take another look at Figure 14.11, where the time course of brain

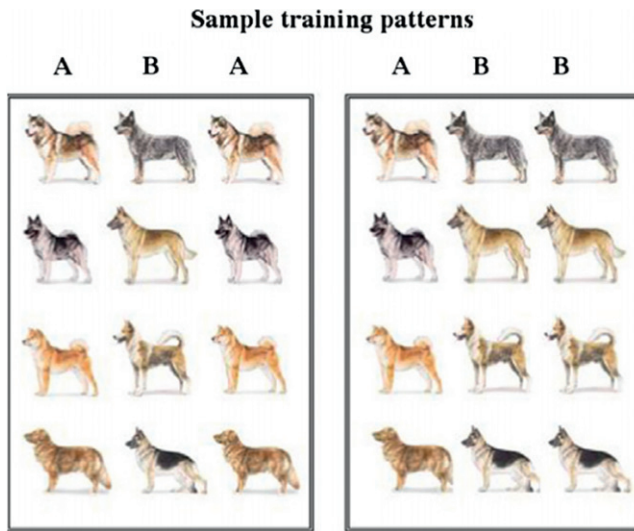


FIGURE 14.15 Examples of stimuli used the study by Saffran and colleagues (2006). Infants were shown dog breed positions: ABA, ABB. Testing revealed that the infants had “learned” these rules in a similar way that they learned language rules. Source: *Saffran et al., 2006*.

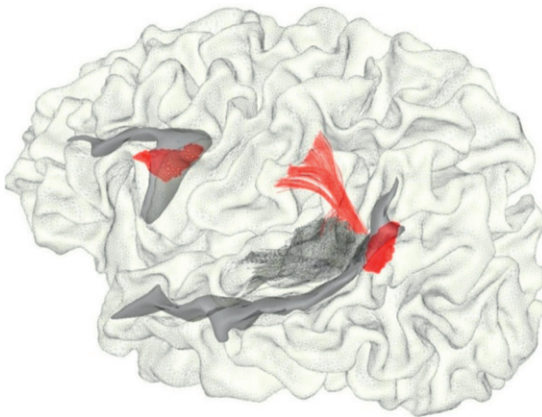


FIGURE 14.16 Language pathway development in infants. Areas shown in red are language pathways in the frontal lobe (left side of figure) and the temporal lobe (right side of figure) that are correlated in terms of their developmental changes. These findings provide evidence that frontal cortex language areas mature earlier than was previously known. Source: *Leroy et al., 2011*.

maturation is shown for different brain regions. Note that the prefrontal cortex is shown to be the last to mature. There is new evidence, again from the laboratory of Dehaene-Lambertz and colleagues, about the maturation of language pathways in the brain. A key finding was that temporal and frontal lobe language pathways are more developed in infants than was earlier thought (Figure 14.16). This study provides intriguing new data that the prefrontal cortex may mature earlier in life than we previously believed.

Language acquisition and speech perception in infancy has been one of the most active areas of developmental cognitive neuroscience. The use of converging methodologies, and frequent comparisons between typical and atypical trajectories of development, make it the domain most likely to see major breakthroughs over the next decade.

4.1.2 *Developing the executive brain: what do babies know?*

A critical aspect of an infant's cognitive growth during the first year of life is the ability to learn about his or her environment. New items will attract the attention of an infant, and he or she will gaze at these items for longer durations than for items that are accustomed to being seen. While it is important for an infant to gaze at a new item, it is also important for an infant to orient to other aspects of his or her environment. The trading effects of looking at new items and shifting attention to other elements in the world around them provide infants both with learning opportunities for understanding features in new items and a wide range of such experiences by changing the focus of their attention, both of which are critical to cognitive development.

The executive control for directing attention to new items, orienting, maintaining goals, and control over reaching movements are thought to require the most anterior portion of the brain: the prefrontal cortex (PFC). As discussed earlier, the frontal cortex shows the most prolonged period of postnatal development of any region of the human brain, with neuroanatomical changes evident even into the teenage years (Huttenlocher, 1990; Giedd et al., 1999). For this reason, it has been the part of the brain most commonly associated with developments in cognitive abilities during childhood.

One of the most comprehensive attempts to relate a cognitive change to underlying brain developments has concerned the emergence of object permanence in infants. Object permanence is the ability to retain an object in mind after it has been hidden by another object or a cover (Figure 14.17). Specifically, Piaget observed that infants younger than around 7 months fail accurately to retrieve a hidden object after a short delay period if the object's location is changed from one where it was previously and successfully retrieved. In particular, infants at this age make a particular perseverative error in which they persistently reach to the hiding location where the object was found on *the immediately preceding trial*. This characteristic pattern of error, called "A not B," was cited by Piaget (1954) as evidence for the failure of infants to understand that objects retain their existence or permanence when moved from view. Beyond about 7 months, infants begin to succeed in the task at successively longer delays of 1 to 5 seconds (Diamond, 1985, 2001).

Diamond and Goldman-Rakic (1989) found that infant monkeys also make errors in an adapted version of Piaget's object permanence task. Similar errors were also seen in adult monkeys with damage to dorsolateral prefrontal cortex (DL-PFC). Damage to other parts of cortex did not have the same effects, indicating a specific role for DL-PFC in this task. Evidence linking this change in behavior to brain development also comes from EEG studies with human infants (Fox & Bell, 1990; Bell, 1992a, b; Bell & Fox, 1992). In these studies, increases in frontal EEG responses correlate with the ability to respond successfully over longer delays in delayed response tasks.

Thus, converging evidence from several sources supports the view that development of PFC allows infants to succeed in the object permanence task. According to Diamond (1991), the critical features of the task carried out by DL-PFC are the ability to retain information over spatial delays and to inhibit prepotent (previously reinforced) responses.

More recent evidence has brought in a new question regarding the development of object permanence in infants: Is it the case that the younger (<7 months) infants who fail at this task actually do understand the concept of object permanence but have just not yet developed

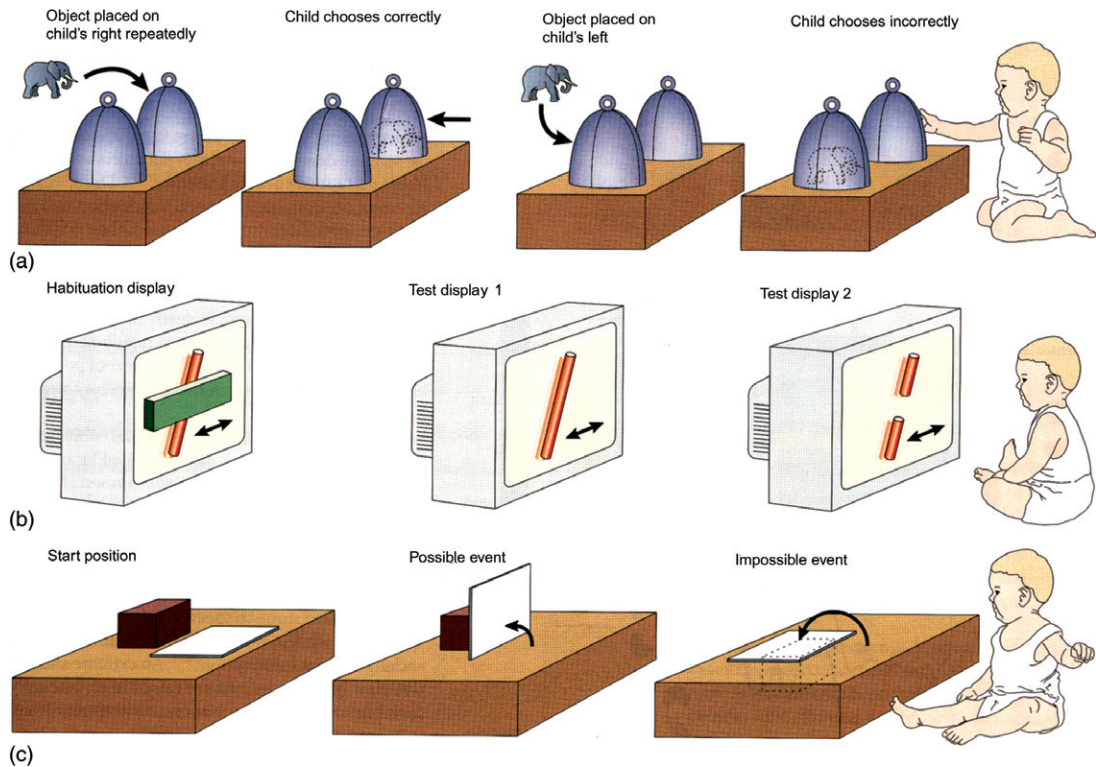


FIGURE 14.17 Behavioral testing in infants. (a) An object retrieval task that infants fail up to 9 months of age. In full view of the infant, the experimenter hides the object in one location and the infant reaches for it successfully. After a few such trials, the experimenter hides the object in a second place, but the infant searches again at the original location (Piaget, 1954). (b) A visual habituation technique can be used to show that infants from as young as 4 months perceive the left-hand figure as a continuous rod moving behind an occluder. Infants dishabituated (found novel) the test display with two short rods, indicating that they perceptually "filled in" the occluded area in the habituation display. Infants under 4 months are only partially successful in such tasks, depending on the complexity of the display. (c) The infant views two event sequences, one possible and one impossible, in which a flap is rotated toward a solid cube. In the "possible" case the flap stops when it comes into contact with the object. In the impossible case the flap rotates through the object. Infants as young as 4 months appear surprised (look longer) when viewing the impossible event, showing that they appreciate that objects are solid and (usually) noncompressible. Source: Johnson, 2001.

their reaching skills adequately to do the task? Studies using eye movement rather than reaching as a measure of an infant response have provided evidence that infants as young as 4–5 months of age can perform successfully in an object permanence task (for example, Lecuyer et al., 1992). Thus it is important to understand both the infant behaviors required and the task demands in order to understand the development of PFC and its role in infant cognition.

Further evidence for the developmental importance of the PFC from early infancy comes from studies of the long-term and widespread effects of perinatal (at birth) damage to PFC: Damage to PFC often results in both immediate and long-term difficulties.

The issue raised at the beginning of this section concerned how to reconcile evidence for continuing neuroanatomical development in the frontal cortex until the teenage years on the one hand (see [Figure 14.12](#)), and evidence for some functioning in the region as early as the first few months of age on the other (see [Figure 14.16](#)). One possible resolution to this issue is that representations that emerge within this region of cortex are initially weak and sufficient only to control some types of output, such as saccades (eye movements), but not others, such as reaching (Munakata et al., 1994). Other plausible resolutions of this issue come from Diamond's (1991) proposal that different regions of frontal cortex are differentially delayed in their development, and Thatcher's (1992) suggestion that prefrontal regions may have a continuing role in the cyclical reorganization of the rest of cortex.

Whether these hypotheses work out or not, there is good reason why some degree of PFC functioning is vital from the first weeks of postnatal life, or even earlier (Fulford et al., 2003). The ability to form and retain goals, albeit for short periods, is essential for generating efforts to perform actions such as reaching for objects. Early and often initially unsuccessful attempts to perform motor actions provide the essential experience necessary for subsequent development.

4.1.3 Developing the social brain: faces and places

One of the major characteristics of the human brain is its social nature. A variety of cortical areas have been implicated in the "social brain," including the superior temporal sulcus (STS), the fusiform "face area" (FFA), and the orbitofrontal cortex. One of the major debates in cognitive neuroscience concerns the origins of the "social brain" in humans, and theoretical arguments abound about the extent to which this is acquired through experience.

One aspect of social brain function in humans that has been the topic of investigation is the perception and processing of faces. There is a long history of research on the development of face recognition in young infants extending back to the studies of Fantz more than 40 years ago (e.g., Fantz, 1964). Over the past decade, numerous papers have addressed the cortical bases of face processing in adults, including identifying areas that may be specifically dedicated to this purpose (see [Chapter 6](#)). Despite these bodies of data, surprisingly little is known about the developmental cognitive neuroscience of face processing.

In a review of the available literature in the late 1980s, Johnson and colleagues (1991) revealed two apparently contradictory bodies of evidence: While the prevailing view, and most of the evidence, supported the idea that infants gradually learn about the arrangement of features that compose a face over the first few months of life, the results from at least one study indicated that newborn infants, as young as 10 minutes old, will track a facelike pattern farther than various "scrambled" face patterns (Goren et al., 1975). The key result of this study was that even though face processing is immature at birth, there is a bias or preference for faces over other visual patterns, and this bias is in place at birth. Newborns also show a preference to familiar faces (such as their mother's) versus unfamiliar faces, providing further evidence that face processing is a critical aspect of social development and that it is in place at birth. One hypothesis is that subcortical structures provide the brain mechanisms for the bias for faces observed in newborns, while slower to develop regions within visual cortex then mature to become more adultlike face processors as the infant grows ([Figure 14.18](#)) (Johnson, 2005b).

Moving beyond the relatively simple perception of faces, a more complex attribute of the adult social brain is processing information about the eyes of other humans. There are two



FIGURE 14.18 Examples of stimuli that have been used to test newborn's preference for face-related stimuli. Some of the stimuli are designed to test the importance of the spatial arrangement (configuration) of a face (eyes, nose, and mouth) and others to test the importance of particular features. Newborns will preferentially attend to patterns that contain the basic configuration of a face (for example, the 2nd, 3rd, and 4th stimuli from the left) as opposed to the other stimuli.

important aspects of processing information about the eyes. The first of these is being able to detect the direction of another's gaze in order to direct your own attention to the same object or spatial location. Perception of averted gaze can elicit an automatic shift of attention in the same direction in adults, allowing the establishment of "joint attention." Joint attention to objects is thought to be crucial for a number of aspects of cognitive and social development, including word learning. The second critical aspect of gaze perception is the detection of direct gaze, enabling mutual gaze with the viewer. Mutual gaze (eye contact) provides the main mode of establishing a communicative context between humans and is believed to be important for normal social development. It is commonly agreed that eye gaze perception is important for mother-infant interaction and that it provides a vital foundation for social development. Evidence that mutual eye gaze is important for newborns comes from a recent study where newborns showed a preference to faces with eyes looking directly at them versus averted eyes (Figure 14.19) (Guellai & Streri, 2011).

Beyond face processing and eye gaze detection, there are many more complex aspects of the social brain, such as the coherent perception of human action and the appropriate attribution of intentions and goals to conspecifics (individuals within your own species, such as human-human interpretation of intentions or goals). Investigating the cognitive neuroscience of these abilities in infants and children will be a challenge for the next decade. One way in which these issues have been addressed is through studying genetic developmental disorders in which aspects of social cognition are either apparently selectively impaired (autism) or selectively intact amid otherwise impaired cognition (Williams syndrome).

The first year of life brings dynamic changes in both behavior and the brain. While we provided separate discussions of the emergence of language, executive functions, and social cognition in this busy first year of life, these three domains of human cognition have complex interactions throughout development. An infant's interest in faces, for example, will help him or her to understand speech. The ability to focus on new objects aids the infant in developing knowledge about the world around him or her. While we do not fully understand the explosive growth of brain processes and their relation to behavior in infants, studies such as the ones we presented here are helping to map the complex correspondence between mind and brain.

4.2 Childhood and adolescence: dynamic and staged growth

While the first year of life represents an unparalleled stage in dynamic human development, many aspects of brain and cognitive growth take years to mature. In this section, we will present results from some studies investigating the development of brain areas



FIGURE 14.19 Examples of the stimuli used in Guellai and Streri’s study on newborn face perception. Newborns showed a preference for (looked longer at) faces when the eye gaze was direct (left photos) as opposed to averted (right photos).

subserving language, executive functions, and social cognition in children and adolescents. While these studies are informative, it is important to bear in mind that relating complex brain activation to performance on cognitive tasks is a highly complex process. For example, it may well be the case that the brain activity that we observe in adults—once a cognitive process has been developed—may tap different brain regions while it is being acquired. Thus simply comparing regions of interest in neuroimaging experiments across groups of children versus adults may not provide us with the level of sensitivity that we require in order to formulate inferences about brain and behavior. Similarly, differing cognitive strategies or coping mechanisms in childhood versus adulthood may also impact the network of brain areas tapped in certain task paradigms.

With those caveats in mind, let’s review the evidence regarding the development of neural systems for language, executive control, and social cognition.

4.2.1 *The linguistic brain: language acquisition*

Language is not a unitary system. In order to express our ideas verbally, we need to progress through stages of formulating the concepts, mapping them onto words in our mental lexicon, accessing our mental grammar to form sentences, and mapping this information onto sound-based representations of the articulation of the ideas we want to express. It makes intuitive sense that, early in life, infants develop their knowledge about language based largely on the *sounds of language* that they hear in their environment. Thus it is not surprising that studies with young infants (less than 12 months) typically focus on the phonology of human language. With older infants, children, and adolescents, studies typically test other aspects of language, such as lexical-semantic (meaning based) and syntactic (grammar based) knowledge.

Do all aspects of language develop in similar ways, with similar brain developmental processes underlying them? This is a question that has been addressed by developmental cognitive neuroscientists investigating the neural substrates of human language. Following is a brief summary of what we have learned so far.

We have previously discussed the use of event-related potentials (ERPs) for measuring the time course of human brain response for stimulus events. Several ERP components have been used to investigate language emergence in infants and young children, and we describe them briefly here:

1. The mismatch negativity (MMN) component shows a negativity at 100–250 ms that reflects the ability for the brain to discriminate between acoustic/phonetic features in sounds.
2. The closure positive shift (CPS) is shown reflecting the processing of intonational boundaries—for example, those at the ends of phrases.
3. The N400 is a negativity at 400 ms that is thought to reflect lexical-semantic processes in word and sentence comprehension.
4. A left anterior negativity (ELAN) that reflects online syntactic processes.
5. The P600 is a positive deflection at 600 ms that reflects processes engaged in syntactic revision and reanalyses.

Friederici (2005) describes the time course of language development in infants and children in a review of the child language literature ([Figure 14.20](#)). According to this review, phonological and intonational processes develop relatively early (birth to 9 months), while lexical, semantic, and syntactic processes develop somewhat later (1–3 years) as infants and young children acquire information at word and sentence levels.

During the first 2 years of life, there is an explosion of language knowledge and abilities as the infant begins to babble, produce simple sounds (“mama”), words (“dog”), and two- to three- word utterances (“want juice”). By age 2, a child can typically produce many words. But what does a 2-year-old understand about the meaning of words? Are they simply mimicking words/sounds they have heard? Or do they have knowledge beyond simple repetition of sound? Researchers have devised clever experimental procedures to investigate the semantic knowledge of infants and young children. One method is to present a picture of an object that the child is familiar with, such as a duck, and then show the word “duck” (congruous condition) or a word that does not match the picture (“cat,” incongruous condition). These careful testing procedures have enabled language researchers to test very young children in order to elucidate their level of semantic knowledge. What do 2-year-olds know about

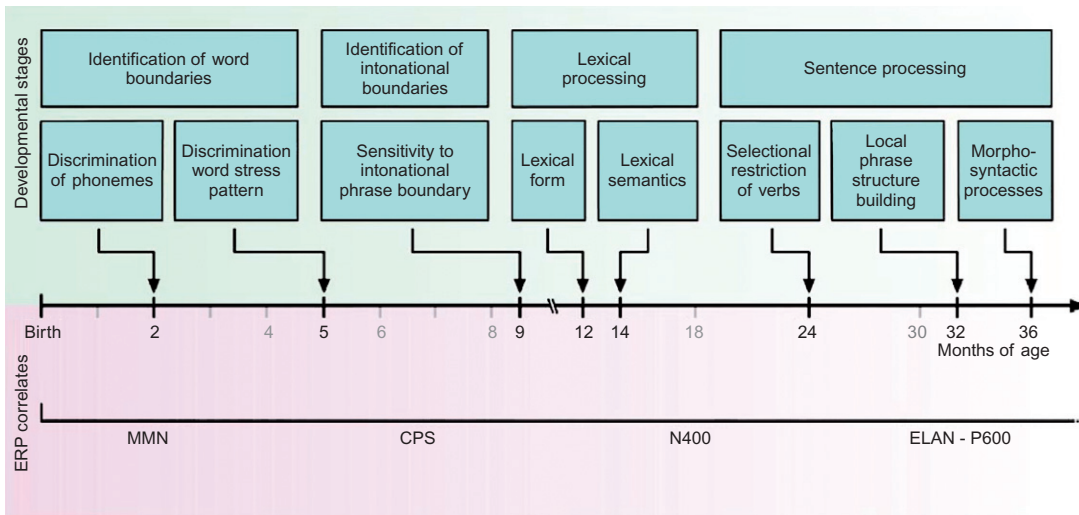


FIGURE 14.20 A schematic overview of the developmental stages of language learning and the ERP correlates that provide the possibility to investigate phonological, semantic, and syntactic processes. Once the basic phonological processes are established, phonemic knowledge is used to identify and represent the first lexical forms (words) and create a larger lexical semantic knowledge base, which is then used to process meaning in sentences. Source: Friederici, 2005.

the grammatical rules of their language? Sentence-level processing was investigated in a sample of 2-year-olds and adults by contrasting sentences that were grammatically well formed (“The lion roars”) to sentences that were not grammatical (“The lion in the roars”). The 2-year-olds were able to discriminate between well-formed and ill-formed sentences, as indexed by the ELAN and P600 components (Figure 14.20).

How do these ERP studies inform us about brain processes for language acquisition in childhood? While these types of studies are in their early stages, these investigations reflect developments in ERP recording techniques and experimental designs that are effective at providing sensitive measures of early language knowledge. While more work is needed to understand fully the complexities of human language acquisition, these studies provide important new data about language knowledge in very young children.

In this section, we have highlighted evidence that very young children have sophisticated knowledge about semantic and syntactic information in spoken language. However, there are many questions that remain unanswered regarding language acquisition. A central issue that remains unresolved is the trading relationship between nature (genetic predisposition for language) and nurture (the role of experience). Other aspects of language acquisition that are currently under investigation are the development of language systems in children who are bilingual or multilingual.

4.2.2 The executive brain: taking cognitive control

Even young infants must learn what information in their world is important and what is unimportant or irrelevant. These learning mechanisms fall under the general category of “cognitive control” and have been the focus of much study in infant and child development.

Recall that in infants, the A, not B, task has been used to investigate the ability to ignore or inhibit irrelevant information and to inhibit prepotent response (Piaget, 1937/1964, 1954; Diamond, 1985). These capabilities become more and more important throughout childhood as a child's environment becomes increasingly complex. Consider a 6-year-old child in a first-grade classroom. This child must be able to pay attention to the teacher or to a task at hand despite the many distractions that surround him, such as children talking, books dropping, chairs scraping. The trading of attentional resources toward relevant aspects of the environment and away from less important aspects is a vital element in development.

In adults, the DL-PFC is implicated as an important cortical region in tasks that tap cognitive control functions. We know from histological and neuroanatomical studies of developing children that the PFC has a prolonged developmental path that does not reach mature, adultlike stages until mid- to late adolescence. Behavioral studies of cognitive control function in children and adolescents have provided evidence for a similar time course in the development of cognitive control abilities. An open question in the field of developmental cognitive neuroscience is if there is any correspondence between these late-to-mature brain regions and the late-developing cognitive control abilities.

Studies of the neural substrates of cognitive control have only recently been undertaken with children. Casey and colleagues (see Casey et al., 2005, for a review) have conducted seminal studies of cognitive control using a combination of fMRI and behavioral methods in order to investigate the neural patterns of brain activation measured while children perform tasks likely to engage PFC regions. In one experiment, they used event-related fMRI while children and adults were engaged in a "go-no go" task (Durstun et al., 2002). In this task, participants had to suppress their response when presented with a particular visual item within an ongoing sequence of stimulus presentations (e.g., one Pokemon character within a sequence of other Pokemon characters). The difficulty of the task was increased by increasing the number of "go" items that preceded the "no go" character. Successful response inhibition was associated with stronger activation of prefrontal regions for children than for adults.

A general finding of Casey and colleagues has been that younger children exhibit broader, more diffuse brain activation for cognitive control tasks as compared to adults. During development, these brain areas mature and the brain activity that correlates to task performance abilities (such as reaction time and accuracy) becomes more focal and fine-tuned. In [Figure 14.21](#), we present a figure from a recent article by Casey and colleagues (2005) reviewing the literature of developmental cognitive control investigations. The general notion of brain activation becoming more focal and defined as a function of a child's age is shown with references to those studies showing increased activation with age and those showing decreased activation with age.

Future work in the investigation of cognitive control and development of PFC in children will need to take into account many other aspects of the prolonged developmental path of the frontal regions and the correspondence to behavior. Some areas of future research may include investigating gender differences in cognitive control functions and related brain activation patterns.

4.2.3 The social brain: face perception in childhood

Human face perception has been the focus of many neuroimaging and behavioral investigations in adults, in infants, and throughout childhood and adolescence. Why is this area of research important to the field of cognitive neuroscience? Investigating brain regions that

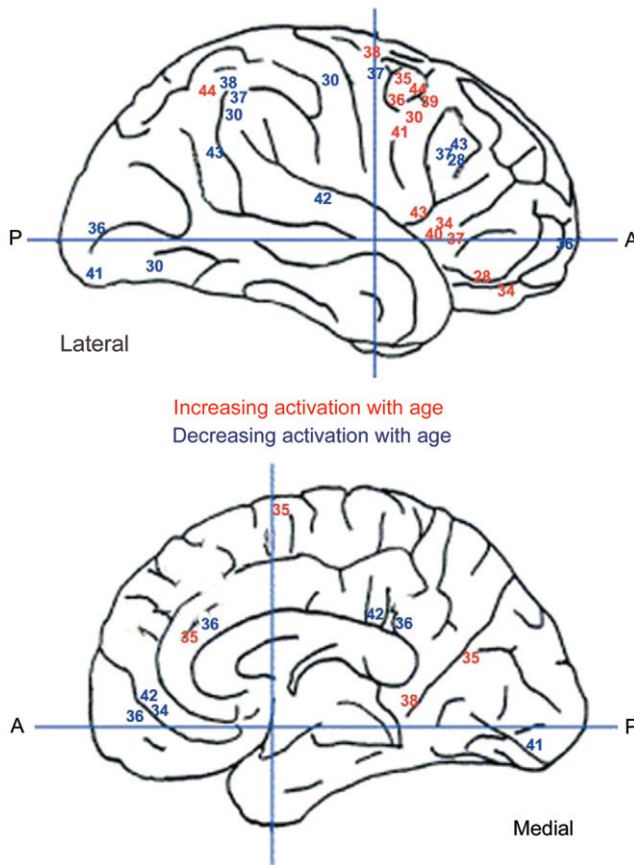


FIGURE 14.21 The development of human cortical function, as measured by contemporary imaging methods, reflects fine-tuning of a diffuse network of neuroanatomical regions. Collectively, developmental neuroimaging studies of cognitive control processes suggest a general pattern of increased recruitment of slow maturing prefrontal cortex (references depicted here in red), especially dorsolateral prefrontal cortex and ventral prefrontal cortex, and decreased recruitment of lower-level sensory regions (references in blue), including extrastriate and fusiform cortex and also posterior parietal areas. This pattern of activity, which has been observed across a variety of paradigms, suggests that higher cognitive abilities supported by association cortex become more focal or fine-tuned with development, whereas other regions not specifically correlated with that specific cognitive ability become attenuated. A = anterior; P = posterior. Source: Casey *et al.*, 2005.

may be specialized for perception of our species-specific faces may shed light on the nature versus nurture debate. Are we predisposed to attend to, focus on, and interpret cues in faces? Or does our vast experience with faces provide the information processing abilities that are not specific to faces but rather utilize visual object perception networks? Studying face processing during development may help us to determine how genetic predisposition interacts with experience.

Recall that, in infants, a bias for human faces, and in particular familiar faces, is present in newborns. How do these processes develop during childhood? As in the case of executive functions shown in Figure 14.21, brain activation for faces appears to be more focal and more face-selective during childhood and adolescence. An fMRI study of brain activation for faces, buildings, and objects with children 5–8 years, 11–14 years, and adults showed an interesting pattern of activations that differed by age (Figure 14.22). The younger (5–8 years) children showed a less selective response for the three categories of images, while older children and adults showed clear differences for face versus buildings versus objects. Together with the findings of Casey shown in Figure 14.21, the early results converge to provide evidence for a gradual change in brain responses that reflects maturational changes during childhood.

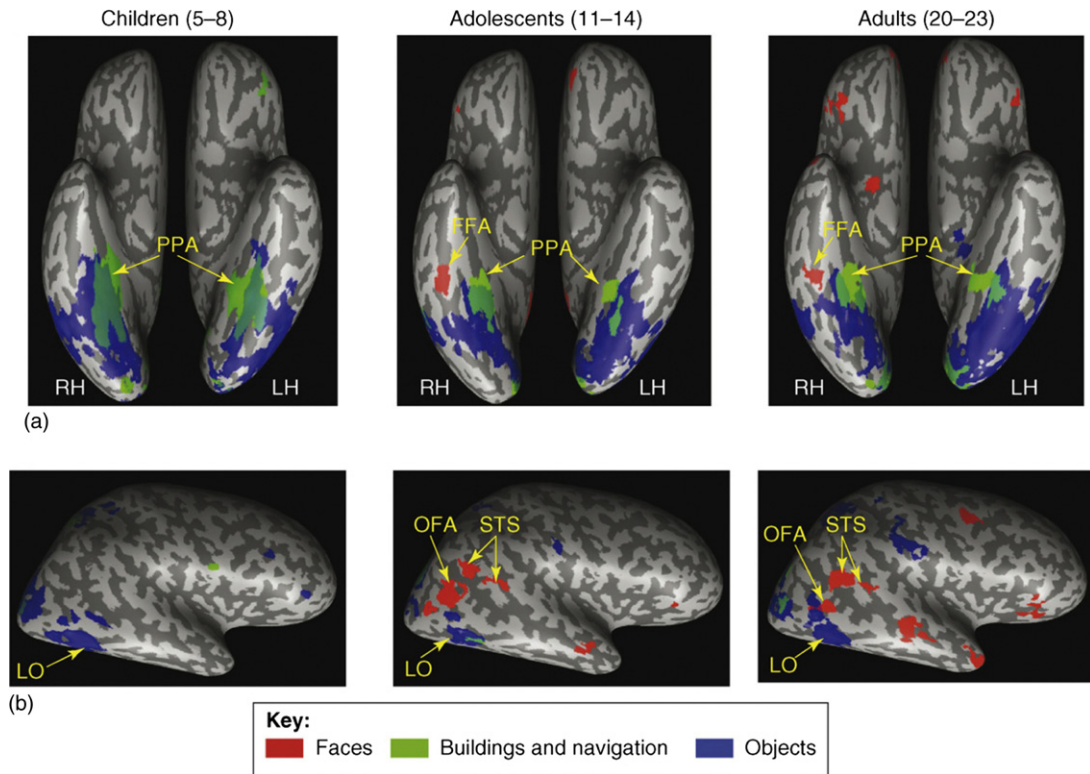


FIGURE 14.22 Brain activation for faces (shown in red), buildings (shown in green), and objects (shown in blue) for children 5–8 years (left panel), adolescents 11–14 years (center panel), and adults (right panel). Results showed that children 5–8 years did not show the face selectivity of older adolescents and adults. Source: *Kadosh & Johnson, 2007*.

What have we learned about the development of language, executive function, and social cognition in childhood and adolescence? One central finding from a variety of data sources is that the cortical regions subserving these higher-order cognitive functions have a prolonged developmental path extending to mid- to late adolescence. We have a wealth of behavioral data showing a similar pattern in tasks that tap more complex and higher-order aspects of these cognitive functions, with task performance not reaching adultlike levels until late adolescence.

An important direction in the field of developmental cognitive neuroscience is to combine methodologies—for example, fMRI with EEG—with behavioral measures in order to provide converging evidence across methodologies and measures regarding aspects of higher-order cognitive function. Combining fMRI with EEG, for example, can provide high-resolution spatial information regarding brain activations coupled with high resolution of the time course of that activation. Another important direction in the field is to conduct longitudinal studies in order to track the development over time of individual children. In this way, early “baseline” measures can be taken, and then the development and change in these measures may be

assessed at specific intervals. Finally, new experimental design approaches with young infants are demonstrating that babies know and understand a lot more about the world around them than we previously thought. New advances in measuring infant cognition and mapping the relevant brain activity will provide important insights into the developmental changes occurring in the first year of life.

5.0 EARLY BRAIN DAMAGE AND DEVELOPMENTAL PLASTICITY

We already mentioned the importance of longitudinal studies for tracking individual progress and outcomes throughout development. This type of study is especially important when assessing the long-term outcome of early (perinatal) brain injury. We have seen in earlier chapters that in adults brain damage due to stroke, disease, or traumatic accident typically leads to deficits in aspects of cognition that are fairly severe, with complete recovery of function unlikely. What happens when brain damage occurs near birth? This question has an important bearing on the nature versus nurture debate. Consider the hypothesis that some brain systems, such as language, have a strong genetic predisposition for their development in specified regions of the brain. If there is early insult to those prespecified regions, will the infant develop language in a typical fashion? Or will language develop in an aberrant fashion due to the early and unrecoverable damage to those brain regions? Alternatively, if experience plays the dominant role in the development of brain regions that become tuned for language function, will the infant develop language in a typical fashion in spite of the early brain damage?

The effects of perinatal brain damage have been extensively investigated in animal studies in the field of neurobiology. The effects of early brain damage and the impact on later cognitive development have been far less studied in humans. One reason for this is that a single, unilateral (in one hemisphere only) pre- or perinatal brain insult is relatively rare. Typically, instances of early brain insult are more global in nature and combine with other neurological complications (Figure 14.23, left panel). In these cases of larger-scale damage coupled with other traumatic events, it is difficult to compare cognitive development to children without this early damage and trauma. In cases where the perinatal damage is limited to a circumscribed region (Figure 14.23, center and right panels), the long-term effects are typically milder. These are the types of cases that we will focus on in this section: early, focal, unilateral brain insult.

While we are just beginning to understand the complexities of early insult on later cognitive growth in humans, a series of longitudinal studies by Stiles and colleagues (2005) shed

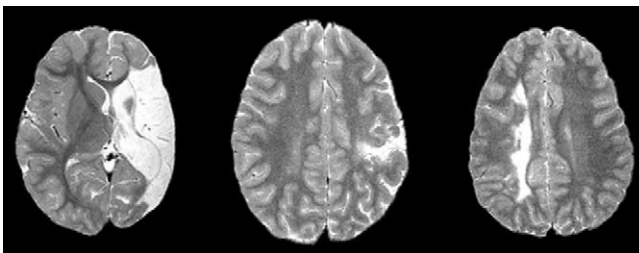


FIGURE 14.23 Large-scale and smaller-scale perinatal brain damage. Structural MRI scans in the axial plane from three children with perinatal brain damage, illustrating different patterns of injury. *Left:* A large unilateral lesion involving most of one cerebral hemisphere. *Middle:* A small lesion confined to one cerebral lobe. *Right:* A deep lesion involving subcortical regions. Source: Stiles et al., 2005.

some light on the long-term effects of perinatal insult, and we highlight some results here (for a review, see Stiles et al., 2005). The San Diego Longitudinal Project (Stiles et al., 2002) is the largest U.S. investigation of the long-term effects of perinatal brain damage. Stiles and colleagues have followed the cognitive development of several hundred children with perinatal brain damage since 1989.

Much of the focus of the investigations by Stiles and colleagues in the San Diego Longitudinal Project has been on language development in children with perinatal brain damage. One key finding is that whereas focal brain damage in language centers in adults (typically through lesions due to stroke) results in long-lasting deficits, this pattern is quite different with infants who suffer perinatal brain damage. While there is typically a delay in early linguistic milestones, such as onset of word comprehension at 9–12 months and word production at 12–15 months, by the age of 5 years, these children have largely “caught up” in linguistic abilities. The important finding, however, is that when tested carefully, there remain some underlying deficits even at the age of 5, especially in complex sentence structures (Reilly et al., 2004). These children with early brain damage do ultimately achieve language competence, but the evidence provided by the longitudinal studies by Stiles and colleagues (reviewed in Stiles et al., 2005) indicates that their language proficiency is in the lower than normal range. Thus while the children do acquire many skills and proficiencies with respect to language, there remain throughout childhood, adolescence, and presumably adulthood, some key deficits due to the very early damage to important brain regions for language acquisition and processing.

Another aspect of cognition that has been the focus of study by the San Diego Longitudinal Project has been spatial cognition. Spatial cognition and the effects produced by adult-acquired brain damage have been the target of many neuropsychological and neuroimaging investigations. The central findings have been that there is a hemisphere asymmetry in the decoding of visual patterns, with the left hemisphere biased for extracting feature (local) information and the right hemisphere biased for extracting configuration (global) information (Figure 14.24).

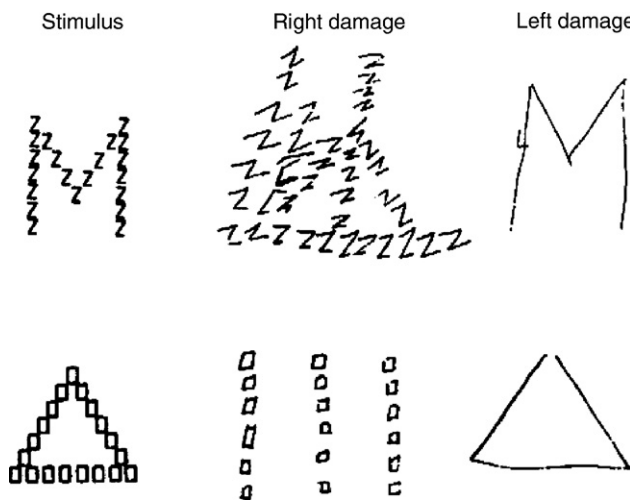


FIGURE 14.24 Global versus local: examples of visuospatial deficits. Examples of memory reproductions of hierarchical form stimuli by adult stroke patients with either right or left hemisphere injury. (Adapted, with permission, from Delis et al., 1986.) The sample stimulus to be copied is shown on the left side of the figure. Center of the figure: patients with right hemisphere damage typically produce the local (detailed) aspects of the stimulus but omit the global (overall) aspects of the stimulus—in this case, the “M” or triangle shape of the stimulus. Right side of the figure: patients with left hemisphere damage typically produce the global aspects of the stimulus but omit the local aspects of the stimulus. Source: Stiles et al., 2005.

Functional MRI studies of typically developing adolescents show that they demonstrate a similar hemisphere asymmetry, with greater right hemisphere occipital-temporal activation for global processing and greater left hemisphere occipital-temporal activation for local processing (Figure 14.25). In stark contrast, a 15-year-old adolescent who had suffered right hemisphere perinatal brain damage showed stronger activation for both global and local processing in the left (undamaged) hemisphere, and a 13-year-old adolescent who had suffered left hemisphere perinatal brain damage showed stronger activation for both global and local processing in the right (undamaged) hemisphere (see Figure 14.25). Thus the fMRI data for

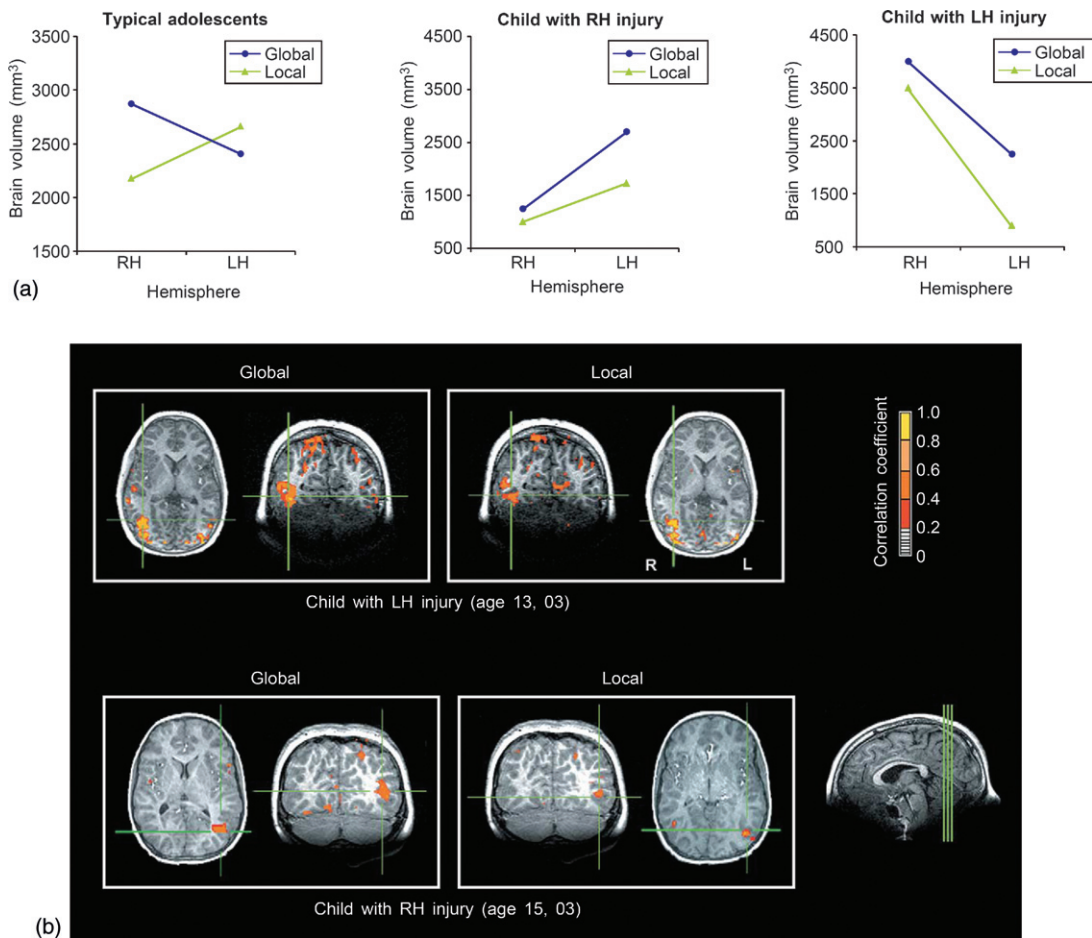


FIGURE 14.25 Global and local processing in the brain. Functional MRI activation data from two teenagers with prenatal focal brain injury on a hierarchical form-processing task, compared with data from typical adolescents. Each child participated in separate imaging runs, where they were asked to attend to either the global or the local level of the stimulus pattern. Unlike typical controls, who show different patterns of lateralization for global and local processing, the two children with lesions showed activation largely confined to the uninjured hemisphere. Activation images for the two children with perinatal brain injury are shown. Source: Adapted from Stiles et al., 2005, with permission.

the two adolescents who suffered perinatal brain damage provide evidence for long-lasting damage to spatial cognition mechanisms. However, they also provide intriguing evidence for a brain system that is highly flexible, with recruitment of neural territory in the undamaged hemisphere for spatial cognition functions.

What have we learned about the long-term effects of early brain damage in the longitudinal studies of Stiles and colleagues? And how do they inform us about the complex and highly interactive roles of nature and nurture in human development? While these efforts are still in the early stages, results to date indicate that early brain damage results in long-term, though typically somewhat subtle, deficits. A second important finding is that despite the early insults and the delays that they typically produce in cognitive development, the children mature and acquire higher cognitive function, although sometimes at the lower than normal level. Cumulatively, these findings provide evidence that some brain systems suffer long-term impairments when damaged, even when the damage occurs at or near birth. This provides some support that some systems have a level of genetic predisposition and can suffer long-term harm when disrupted. On a brighter note, these findings provide evidence for significant amounts of early brain plasticity so that the cognitive functions that suffer early damage develop in an alternative manner.

6.0 SUMMARY

In this chapter, we tracked the stages of human development from early embryo to infant to adolescent. While the field of developmental cognitive neuroscience is still a very young one, nevertheless, the findings presented in this chapter demonstrate the answers to important questions about human brain development and the correspondence to cognition. An overarching topic of much debate in the field of human development is the role of nature versus nurture. From the data presented here, you see that at each stage of human development there are important genetic effects and biological constraints at work in the unfolding of the human brain and mind. Similarly, at each state there are critical effects of the surrounding environment, whether at the level of the cell, the system, or the brain.

The advent of new techniques for noninvasively studying human development has provided the means to address new questions about cognitive development, such as what does a baby know before birth? Does an infant understand the grammar of language? How does the sense of self develop in an infant and a child? What are the long-term effects of focal brain damage? These and other questions will be addressed in future studies investigating the unfolding complex pattern of human brain development and its relation to cognition.

7.0 STUDY QUESTIONS

1. In what ways have neuroimaging techniques changed the way infant and child development is investigated?
2. What does the term *bidirectional influences* refer to in human development? Why is it an important concept?

3. Provide an example of a nature and nurture interaction that occurs before birth (prenatally).
4. What are some effects of maternal use of alcohol, tobacco, and marijuana on an unborn baby?
5. What brain regions develop and mature early in childhood? What regions develop later in childhood?

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Glossary

- acoustical analysis** (uh-KOO-sti-kul uh-NAL-ih-sus; Greek *akoustikos*—of hearing): The process of interpreting physical sound energy, whether linguistic, musical, or sounds in the environment (as in a door slamming or a car starting). See Chapter 11.
- action potential** (AK-shun po-TEN-shul): In neurons, an electrochemical signal beginning near the cell body and traveling down the axon to the synaptic terminal. Also called a “spike” or “neuronal firing.” See Chapter 3.
- alpha waves** (AL-fa WAY-vz; first letter of Greek alphabet): A regular electromagnetic wave detected in the brain or on the scalp and apparently reflecting the activity of large populations of neurons. Alpha waves have a frequency of 7.5 to 13 Hz and originate predominantly from the occipital lobe during periods of waking relaxation with the eyes closed. Conversely, alpha waves are decreased when the eyes are open, as well as by drowsiness and sleep. See Chapters 5 and 8.
- amnesia** (am-NEE-zhuh; from Greek *a-mn-sia*—not memory): A loss of memory. Two types are anterograde (a loss of memory after the time of the brain injury) and retrograde (a loss of memory before the time of the brain injury). See Chapter 9.
- amygdala** (uh-MIG-da-la; from *amygdale*—almond): The amygdalas are two small, almond-shaped masses of neurons located inside the tips of the temporal lobes. They are considered part of the limbic system and play major roles in emotions like fear and trust, as well as in learning. See Chapter 13.
- anterior** (ann-TEER-ee-er; from *ante*—in front of): Located in front of something. See Chapter 1 and the Mini-Atlas.
- anterior cingulate cortex** (an-TEER-ee-er SIN-gyu-lut COR-teks; from Latin *ante*—before, in front of; Latin *cingulum*—girdle; Latin *cortex*—bark): The frontal part of the cingulate cortex. The anterior cingulate cortex is involved in executive functioning. See Chapters 2 and 12.
- anterior commissure** (an-TEER-ee-er KA-mih-shur; from Latin *ante*—before, in front of): A large bundle of nerve fibers connecting the two cerebral hemispheres. See Chapter 4.
- anterograde amnesia** (AN-teh-ro-grayd am-NEE-zhuh; from New Latin *antero*—forward; Greek *a-mne-sia*—not memory): A form of amnesia in which events after the brain injury are not encoded in long-term memory, although events may be recalled from the period before the injury. See Chapter 9. See **retrograde amnesia**.
- aphasia** (AY-PHAY-zha; from, *a*—without; Latin *phasia*—speech): A loss of language function due to brain injury, such as damage to Broca’s area, for speech production, or Wernicke’s area, for speech understanding. See Chapters 1, 7, and 11.
- arcuate fasciculus** (AR-cue-ate fa-SIK-u-lus; Latin for arched bundle): A bundle of axonal fibers, especially the ones connecting Broca’s and Wernicke’s areas in the left hemisphere. See Chapter 4.
- area MT**: A part of visual cortex that represents visual motion. See Chapter 6.
- array** (uh-RAY): 1. A two-dimensional grid of sensory receptors, such as the retina. 2. A two-dimensional grid of higher-level elements in the visual hierarchy. Many “layered” brain structures can be considered to be such arrays. See Chapter 3.
- artificial neural net** (ar-ti-FI-shel NOOR-el NET; from Greek *neuron*—nerve): Also known as ANNs or neural models, artificial neural nets are simulated, simplified models of brain functions. Most are relatively small in scale. However, they are important for understanding the principles of neural computation. See Chapter 3.
- associative process** (uh-SO-see-a-tiv PRA-ses; from Latin *ad-* + *sociare*—to join): A process in which one or more sensory and/or response events are linked in the brain. See Chapter 9.
- attention** (a-TEN-shun; from Latin *attende-re*—to stretch out): Selection of some sensory, cognitive, or motor events to the exclusion of others. Attention is often taken to involve a focus on certain conscious events. Also see selective attention. See Chapter 8.
- attention network task (ANT; a-TEN-shun NET-werk TASK)**: A generalization of the **flanker task**, a tool for studying visual attention. The ANT allows testing of three separate aspects of attention: alerting before an expected signal, orienting to a specific location in space where the target is expected, and executive attention to act against expectations set up by the task. See Chapter 8.

- auditory cortex** (AW-di-tor-ee kor-teks; from Latin *auditorius*—pertaining to one who hears; Latin *cortex*—bark): The parts of the cerebral cortex involved in processing sounds, such as Wernicke's area and Heschl's gyrus. See Chapter 7.
- auditory scene analysis** (AW-di-tor-ee SEEN uh-NAL-ih-sus): The process by which the auditory system segments and organizes the listening environment. See Chapter 7.
- autonomic nervous system (ANS)** (aw-to-NOM-ic NER-vus SIS-tem; from Greek *neuron*—nerve): The division of the peripheral nervous system that acts to maintain homeostasis and to regulate rest and activity. Physiological activities controlled by the ANS such as blood pressure and sweating are generally unconscious and nonvoluntary. See Chapter 4.
- automatic process** (au-to-MA-tic PRAH-ses): A highly practiced skill or habit that can be performed with minimal conscious involvement and voluntary effort. See Chapter 3.
- axon** (AK-son): A long, slender branch of a nerve cell (neuron) that conducts electrical impulses away from the cell body. See Chapter 3.
- Baron-Cohen, Simon** (b. 1958): Autism researcher who proposed that young children develop a **theory of mind** capacity, composed of four skills: detection of intentions of others, detection of eye-direction, shared attention with others, and implicit knowledge about others. See Chapter 13.
- basal ganglia** (BAY-zel GAN-gee-uh; from Greek *basis*—step, base; Greek for ganglion 'tumor on or near tendons'): A large cluster of subcortical structures just outside of each thalamus, involving motor control, automaticity, cognition, emotions, and learning. See Chapter 4.
- behaviorism** (bi-HAY-vyer-ism): A philosophy of psychology proposing that all things organisms do, including acting, thinking, and feeling, should be regarded as behaviors. See Chapter 1.
- beta waves** (BAY-tuh WAYVZ; second letter of Greek alphabet): A band of irregular electromagnetic waveforms detected in the brain or on the scalp, and apparently reflecting the activity of large populations of neurons. The beta band has a frequency above 18-25 Hz and is associated with normal waking consciousness. Low-amplitude beta waves with multiple and varying frequencies often are associated with active, busy, or anxious thinking and active concentration. See Chapter 5.
- binocular disparity** (bih-NOC-u-ler dis-PAR-eh-tee; from Latin *bi*—two; Latin *oculus*—eye; Latin *disparare*—to separate): The difference in perceived location of an object seen by the left and right eyes, resulting from the eyes' horizontal separation. The brain uses binocular disparity to obtain depth information from the retinal image in both eyes. See Chapter 6.
- binocular rivalry** (bih-NOC-u-ler RYE-vel-ree; from Latin *bi*—two; Latin *oculus*—eye): The alternating perception that occurs when a different pattern is shown to each eye and the brain cannot fuse them into a single, coherent percept. Instead, awareness of each eye's input appears and disappears for a few seconds. See Chapters 6 and 8.
- bistable perception** (BYE-STAY-bel per-SEP-shun; from Latin *b*—two): Sensory events that alternate between two perceptual interpretations. See Chapter 6.
- blindsight** (BLIND-site): A type of brain damage in which patients can report some visual events with no subjective sense of seeing them, due to impairment of the first cortical area of the visual system, area V1. See Chapter 6.
- blood-oxygen-level-dependent (BOLD) activity** (BLUD OKS-eh-gen LEV-el dee-PEN-dent ak-TI-vi-tee): A magnetically induced physical signal that reflects the flow of oxygen in the bloodstream in specific regions of the brain. The BOLD signal is the physical source for functional magnetic resonance imaging. See Chapter 5.
- brainstem** (BRAYN-stem): The lower part of the brain, connecting to the spinal cord. All major motor and sensory systems pass through it, including the optic and auditory nerves. The brainstem also regulates cardiac and respiratory functions and maintains conscious waking, slow wave sleep (SWS), and REM dreams. See Chapter 4.
- Broadbent, Donald** (1926–1993): British cognitive psychologist who developed the influential concepts of selective attention and working memory. See Chapter 2.
- Broca, Pierre-Paul** (1824–1880): A French surgeon who studied a brain-damaged patient with expressive aphasia, the inability to speak, while being able to understand speech. After the patient's death he was able to conduct a postmortem identifying the damaged region as the left inferior frontal gyrus, now called Broca's area. See Chapter 1.
- Broca's area** (BRO-kas AIR-ee-a): The left inferior frontal gyrus, or its posterior segment, reported by Pierre-Paul Broca in 1861 to be responsible for the deficit of a patient who could not speak but had preserved speech understanding. Other functions have since been attributed to Broca's area. See Chapters 1, 7, and 11.
- Brodmann's areas** (BROD-mans AIR-ee-uh): About 100 cortical regions defined and numbered by German neurologist **Korbinian Brodmann**, originally based

on the microscopic anatomy of **neurons** in different patches of the cortex. They are still widely used for cortical localization, and Brodmann's areas generally have distinctive functions. See Chapter 5.

cell assemblies (SEL uh-SEM-blees): Also called Hebbian cell assemblies, these are active networks of related **neurons** representing some sensory input or similar event. According to Donald O. Hebb's 1949 hypothesis, "neurons that fire together, wire together," so that simultaneous firing causes the **synaptic** links in a cell assembly to grow stronger. See **Hebbian learning**. See Chapter 3.

central executive (CEN-trel eks-EK-yoo-tiv; from Latin *centrum*—center): Brain processes for planning, decision making, abstract thinking, rule acquisition, initiating and inhibiting actions, resolving goal conflicts, and flexible control of attention. These functions relate to **working memory** and tend to involve the **frontal lobes**. See Chapters 2, 8 and 12.

central nervous system (CNS; SEN-trel NER-vus SIS-tem; from Latin *centrum*—center; Latin *nervus*—sinew, nerve): The brain and spinal cord. All neurons outside of the CNS are considered to be the **peripheral nervous system** (PNS). See Chapter 4.

central sulcus (SEN-tral SUL-cus; from Latin *sulcus*—groove): Also called the central fissure, this fold in the **cerebral** cortex is a prominent landmark of the brain that separates the **parietal lobe** from the **frontal lobe** and the **primary somatosensory cortex** from the **primary motor cortex**. The central sulcus is a clear dividing line between the input- and output-related areas of cortex. See Chapter 1.

cerebellum (ser-e-BEL-em; from the Latin word *cerebrum*—brain, *cerebellum* means "little brain"): A major region of the brain located just below and to the rear of the occipital lobe of the cerebral cortex. The cerebellum plays an important role in the integration of sensory perception, fine motor control, and sensorimotor coordination. Recent evidence shows cognitive involvement as well. See Chapters 1 and 4.

cerebral cortex (suh-REE-bral KOR-teks; from Latin *cerebrum*—brain; Greek *cortex*—bark): The outer surface of the great cerebrum, the largest part of the human brain, divided into two symmetrical **cerebral hemispheres**. Most of the cortex has six distinctive cellular layers, containing cell bodies with a gray appearance. But its long-distance nerve cells send out axons to other parts of the cortex, to the thalamus, and to other brain regions, which become covered with white supportive cells (**myelin**). As a result, a vertical cut of the cortex appears to the naked eye to have a thin, gray outer layer and a white

inner mass, called the "gray matter" and "white matter," respectively. The cerebral cortex plays a key role in sensory analysis, spatial location, speech perception and production, **memory**, **attention**, emotion, motivation, action planning, voluntary control, thought, **executive functions**, and **consciousness**. See Chapters 1 and 4.

cerebrospinal fluid (CSF) (suh-ree-bro-SPEYE-nel floo-id; Latin *cerebrum*—brain): The internal circulation of the spine and brain. CSF allows for a protected flow of molecules and cells that is not exposed to the blood stream. See Chapter 4.

cerebrum (suh-REE-brum; Latin for *brain*): See **cerebral cortex**.

chunking A way to make efficient use of short-term **memory** limitations by condensing large amounts of knowledge into a small symbolic units, rules, or regularities, called "chunks." In natural language nouns can be considered to be chunks, since they allow us to refer to large bodies of knowledge by single words. See Chapter 2.

cingulate cortex (SIN-gyu-lut KOR-teks; from Latin *cingulum*—belt; Latin *cortex*—bark): A part of the **cortex** on the medial (inner) surface of each hemisphere. It is involved in executive functions, the resolution of conflicting goals, and emotion. See Chapter 4.

cognitive neuroscience (KOG-ni-tiv NOOR-o-SI-ens; from Latin *cognoscere*—to know): An emerging integration of two previously separate fields of science, cognitive psychology and neuroscience. Most research in cognitive neuroscience makes use of psychological methods simultaneous with brain activity recording. See Chapter 1, "Introduction."

computed tomography (kom-PYOO-ted tom-OG-reh-fee; from Latin *computare*—to consider; Greek *tomos*—slice; Greek *graphein*—writing): Abbreviated as **CT**. Physiological recordings in which a three-dimensional image of a body structure (such as the brain) is constructed by computer from a series of slice images. See Chapter 5.

confabulation (kon-fab-yoo-LAY-shen; from Latin *fabula*—story): A neurological symptom in which false memories or perceptions are reported with no intention to lie. See Chapter 9.

connectionism (keh-NEK-shun-ism; from Latin *com-* + *nectere*—to bind together): The study of artificial or biologically based neural networks. See Chapter 3.

consciousness (KON-shes-ness; from Latin *com-*—together; *scientia*—knowledge): Awareness, wakefulness. **Consciousness** implies being sensitive and responsive to the environment, in contrast to being asleep or in coma. See Chapters 1 and 8.

- consolidation hypothesis** (kon-SOL-ih-DAY-shun high-POTH-uh-sis): The process by which new memories are transformed into long-term **memory** traces. Memories may be stored in the same areas of the brain that support active moment-to-moment functions like perception and speech control. Consolidation may involve synaptic changes in these brain regions, which make active neuronal connections more efficient. See Chapters 2 and 9.
- contralateral** (KON-tra-LAT-er-el; Latin for “against the side”): The opposite side of the body or brain. See Chapters 1, 2, and 4. See **ipsilateral**.
- coronal** (keh-RONE-el; from Latin *corona*—crown): A crown-shaped vertical slice of the brain that divides it into **anterior** and **posterior** halves. See Chapter 1.
- corpus callosum** (KOR-pus kal-OS-um; from Latin *corpus*—body; Latin *callosum*—tough): A massive fiber bridge between the right and left hemispheres, consisting of more than 100 neuronal axons. It appears white when cut because the axons are covered by white **myelin** cells. See Chapters 1 and 4.
- cortex** (KOR-teks): See **cerebral cortex**.
- cortical column** (KOR-ti-kel KAW-lum; from Greek *cort*—skin, husk; Latin *columna*—pillar): A barrel-shaped slice of the six surface layers of **cortex** that often contain closely related **neurons**. Columns are about 0.5 mm in diameter and 2.5 mm in depth. They may be clustered into **hypercolumns**, which may be part of even larger clusters. See Chapter 4.
- creole** (KRAY-ole): A true language that children spontaneously evolve in multilingual communities. Creoles often are encountered in island communities where language communities overlap. “Creoles” are contrasted with “pidgins,” which are dialects typically spoken by adults as a second language consisting of simplified phrases rather than full grammatical languages: for example “me go now” as opposed to “I am going now”. Creoles are remarkable because they exhibit a full-fledged grammar, unlike pidgins. The spontaneity with which they arise suggests that human infants and children may be equipped with a biological language capacity with universal features. See Chapter 11.
- Darwin, Charles** (1809–1882): English naturalist who was among the first in modern times to make a persuasive case that all living species emerged from common ancestors over very long stretches of time by “survival of the fittest” and the most reproductively successful. Darwin also published important observations about emotional expressions in humans and animals. See Chapter 1.
- declarative memory** (deh-KLAR-a-tiv MEM-ree; from Latin *declarare*—Latin *declarare*, from *de-* ‘thoroughly’ + *clarare* ‘make clear.’): The capacity to recall facts and beliefs. A kind of **explicit memory**. See Chapters 2 and 9.
- déjà vu** (DAY-zha VOO; French for “already seen”): A feeling that one has lived through the present moment before. See Chapter 9.
- delta waves** (DEL-tuh WAYVZ; fourth letter of Greek alphabet): A band of slow, high-amplitude electromagnetic waveforms associated with deep sleep, and recorded in the brain or on the scalp, apparently reflecting large populations of neurons. Delta generally is considered to be less than 2.5 Hz. It coexists with waking EEG as well, but becomes visible in the raw (unprocessed) EEG only when delta predominates in sleep and drowsy states. See Chapter 5.
- dendrite** (DEN-drite; from Greek *dendritēs* ‘treelike’): One of numerous thin, branched micron-level tubes extending from the cell body of a **neuron**. Dendrites typically receive synaptic stimulation from other neurons, and therefore serve as the input branches of the neuron. See Chapter 3.
- Descartes, René** (1596–1650): A French philosopher, mathematician, scientist, and writer who spent most of his adult life in the Dutch Republic. Descartes has been dubbed the “Father of Modern Philosophy” and was also a careful student of the brain. He often is considered the originator of modern mind/body philosophy. See Chapter 1.
- developmental cognitive neuroscience** (deh-vel-op-MEN-tel COG-ni-tiv NUR-o-si-ens): The study of the normal growth of the brain and its mental capacities. See Chapter 14.
- diencephalons** (die-en-SEF-a-lon; from Greek *dia*—through; *enkephalos*—brain): The part of the brain that contains the **thalamus**, **hypothalamus**, and the posterior half of the **pituitary gland**. See Chapter 4.
- diffusion tractography** (di-FYOO-zhen trak-TOH-greh-fee; from Latin *diffusus*—scatter; *trahere*—to pull; Greek *graphein*—writing): A brain imaging technique that tracks the diffusion of water molecules in order to trace the major neuronal pathways of the brain. See Chapter 5.
- discourse** (DIS-kors): A connected series of utterances, a conversation. Used by linguists to reflect more than a series of sentences, rather a conversation with a theme and with intents. See Chapter 11.
- domain specificity** (do-MANE spes-i-FIS-ih-tee): Functional specificity of brain regions or mechanisms. The idea that each cognitive function may have its own region or network of brain regions, rather than general-purpose brain mechanisms with multiple cognitive functions. See Chapter 12.
- dorsal** (DOR-sel; from *dorsum*—back): The upper part of a brain structure, also called **superior**.
- dorsolateral prefrontal cortex** (DOR-so-LAT-er-el pree-FRON-tal KOR-teks; from Latin *dorsum*—back;

latus—side; *pre*—in front of; *frons*—the forehead; Greek *cortex*—bark): Prefrontal region involved in motor planning, executive control, self-regulation, emotion, and **working memory**. See Chapters 2 and 12.

dynamic causal modeling (die-NAM-ic KOS-el MO-del-ing; from Greek *dynamikos*—powerful; Latin *causa*—cause; Latin *modulus*—small measure): A method for interpreting brain data, such as **functional magnetic resonance imaging** (fMRI), that helps to interpret causal relationships among brain activities during a specified task. See Chapter 5.

Edelman, Gerald M. (b. 1929). American immunologist and neurobiologist who won the Nobel Prize for his work on the structure of antibody molecules. Edelman developed the theoretical framework of Neural Darwinism, which applies Darwinian selectionist principles to the brain, in contrast to the instructionist principles of conventional computers. See Chapter 3.

electroencephalography (EEG; eh-LEK-tro-en-sef-eh-LOG-reh-fee; from Greek *e-lektron*—sunlight; *en-* + *kephale*—in the head; *graphein*—writing): Electrical activity that typically is recorded on the scalp and sometimes on the surface of the **cortex**, reflecting the electromagnetic field of large numbers of active neurons. See Chapter 5.

empathy (EM-path-ee; from Greek *empathia*—passion): The capability to share one's feelings and understand another person's. See Chapter 13.

epigenesis (ep-ih-GEN-eh-sis; from Greek *epi*—after; Greek *genesis*—birth, origin): Non-DNA factors that shape cells during gestation (pregnancy) and after birth. Contrasted with the classical Central Dogma of molecular biology, in which DNA is recoded into transfer RNA, which ends in the production of proteins for the structure and functions of all cells. Epigenesis implies a flow of causality in the opposite direction. For example, numerous physiological and environmental factors can influence whether specific genes (DNA) are expressed or not. DNA is the primary molecule that encodes phenotypes, passing the plan for a species from one generation to the next. But non-DNA factors can influence the activation and silencing of DNA, the on/off switches. See Chapter 14.

episodic memory (ep-i-SOD-ic MEM-ree; from Greek *episeidos*—coming in besides): **Memory** for conscious experiences, especially those that can be explicitly recalled, such as times, places, events, associated emotions, and other contextual knowledge. The formation of new episodic memories requires the **medial temporal lobe**, especially the **hippocampal region** in combination with the **cerebral cortex**. See Chapters 2 and 9.

evoked potential (EP; ee-VOKD puh-TEN-shul; from Latin *evocare*—to call forth; *potentia*—power): Also called **event-related potential** (ERP). A quite stereotypical electrical voltage pattern obtained from the brain, after averaging a time-locked voltage to a stimulus or other known event. Traditionally, the EP was obtained by averaging the stimulus-locked EEG over numerous trials. Though the exact brain sources of EPs are still debated, they are highly sensitive to cognitive and emotional variables. See Chapter 4.

executive attention (ek-ZEK-u-tiv a-TEN-shun): Also called **voluntary**, **goal-directed**, or **top-down attention**. The act of voluntarily focusing on one stream of conscious events while ignoring others. Also see **selective attention**, **stimulus-driven attention**. See Chapters 8 and 12.

executive function (ek-ZEK-u-tiv FUNK-shun): Also called **executive control** or **frontal lobe function**. Capacities such as planning, cognitive flexibility, voluntary action, abstract thinking, rule acquisition, initiating correct actions and inhibiting incorrect ones, impulse control, and emotional regulation. See Chapter 12.

explicit memory (eks-PLI-sit MEM-ree; from Latin *explicitus*—clear): A type of **memory** involving conscious, intentional recollection of stored experiences, and knowledge. See **implicit memory**, **implicit learning**. See Chapters 2 and 9.

Fechner, Gustav (1801–1887): German physicist, mathematician, and pioneer in psychophysics. Fechner claimed to have solved the mind-body controversy when he demonstrated a general logarithmic relationship between subjective sensory intensity and physical stimulus intensity across many different sensory modalities. See Chapter 1.

feedback (FEED-bak): 1. In goal-guided systems, a signal from the environment indicating the degree of error in achieving the goal. 2. In neuroscience and psychology, an environmental signal reflecting some neuronal event. This kind of neurofeedback often allows people to learn to control otherwise spontaneous neuronal activities. 3. In neural networks, a flow of information returning an output signal to the input layer of the network. Some theorists make a strong distinction between **feedback** and **reentrant** signaling in the **thalamo-cortical** system of the brain. See **Neural Darwinism**. Chapters 3 and 9.

feedforward (feed-FOR-werd): 1. Signal passing from a simpler to a more complex stage of processing. 2. In sensorimotor guidance, preparing an internal action trajectory to obtain more precise feedback when the action is executed. This strategy is used in fast movement control in birds and humans, and even in

- machines like aerodynamically unstable jet planes.
3. In neural networks, passing information from earlier to later layers of the network.
- fetal alcohol syndrome** (FEE-tel AL-ko-hol SIN-drum): (FAS). Brain damage in a fetus due to the mother's alcohol consumption, a major health risk. See Chapter 14.
- flanker task** (FLANK-er TASK): A tool for studying visual attention, in which the subject is asked to respond as quickly as possible to a target at the center of gaze or one located off-center by a known distance. The target is flanked by distracting stimuli, such as arrows or letters. The flanker task permits quantitative assessment of the subject's speed and accuracy in shifting attention to an expected or unexpected position of the target. Moving attention in an unexpected direction is taken to require **executive attention**, since it must override the prepared, expected shift. Flanker tasks generally require subjects to avoid voluntary eye movements, so that any change in accuracy or speed in response to a target can be attributed to **implicit** shifts of attention. See Chapter 8.
- flash suppression** (FLASH suh-PRESH-en): A variant of the binocular rivalry task, in which an image presented to one eye is suppressed by a flashed image to the other eye. See Chapter 8.
- Fourier analysis** (FOOR-ee-ay uh-NAL-a-sis): Named after French mathematician and physicist Joseph Fourier, who showed that any complex function can be decomposed into a finite set of sine and cosine functions. In music, for example, this implies that any complex sound can be decomposed into a set of pure tones (sine waves). Fourier analysis is routinely applied to decompose EEG and other complex brain signals into frequency bands. See Chapter 5.
- Freud, Sigmund** (1856–1939): Austrian physician and neurologist who founded the psychoanalytic school of psychology and was a highly influential cultural figure. Freud is best known for his theories of the unconscious mind and for creating the clinical practice of psychoanalysis. He was also an early neurological researcher who developed an early neural network model and discovered a new chemical stain—gold chloride—which allowed certain brain-stem neurons to stand out clearly under the microscope. Although many of Freud's ideas have fallen from favor, some brain phenomena, like the role of the frontal lobes in regulating emotional impulses and goal-conflicts, are broadly consistent with his point of view. See Chapter 1.
- frontal lobe** (FRON-tal lobe): A large region of cortex located at the front of each cerebral hemisphere and positioned forward of the **parietal lobes** and above and in front of the **temporal lobes**. The executive functions of the frontal lobes include the ability to anticipate the consequences of actions, to plan and make decisions, to speak, to override inappropriate impulses and resolve conflicting goals, to understand the mental states of others, and to hold information in working memory. See Chapters 1 and 4.
- functional fixedness** (FUNK-shun-el FIKS-ed-ness): A cognitive set that tends to block a person from novel ways of acting, perceiving, or solving problems. See Chapter 10.
- functional magnetic resonance imaging** (fMRI; FUNK-shun-el mag-NET-ic REZ-nence IH-ma-jing): fMRI uses a combination of the MRI signal—which provides images of the brain with high anatomical accuracy—with measures to assess sensory, motor, and cognitive processes. fMRI experiments typically use a subtraction method where brain activation for one experimental condition is literally subtracted from another. Early fMRI studies employed a task + resting state method where for example brain activation for a particular task would be compared for activation during a rest (no task) condition. fMRI methods have continued to change and evolve and currently there are many other methods employed that are more sensitive to providing information about complex cognitive processes. fMRI helped to make cognitive neuroscience possible. See Chapter 5.
- functional redundancy** (FUNK-shun-el ree-DUN-den-see): Built-in backup functions in a system to prevent the complete failure of critical functions. For example, mammals have two lungs so that if one fails, the organism still has one lung to breathe. The brain has multiple redundant capabilities. See Chapter 3.
- fusiform face area** (FFA; FYOO-ze-form; from Latin *fusus*—spindle, after its shape): A specialized region in the **medial temporal lobe** that responds selectively to visual faces compared to other objects. See Chapters 6 and 14.
- Gage, Phineas** (1823–1860): A historic brain damage patient, whose railroad accident demonstrated remarkable spared cognitive capacities in spite of severe damage to the frontal lobes. Gage was a railroad foreman who had a two-foot-long thin tamping iron shot through the upper orbit of the left eye and out through the medial scalp, when an unstable dynamite charge exploded unexpectedly. Although Gage appeared to have no loss of perception, motor control, or speech, his personality changed in ways that have come to typify frontal lobe damage, especially a major loss of impulse control and long-term motivation. See Chapters 2 and 12.
- gamma waves** (GAM-a WAYVZ; third letter of Greek alphabet): A band of fast, low-amplitude electromagnetic waveforms associated with wakefulness and active thinking, and recorded in the brain or on the scalp, apparently reflecting the activities of large

populations of neurons. The gamma band is thought to be centered near 40 Hz, ranging from 25 to 60 Hz. However, higher frequency waves are sometimes labeled gamma as well. Gamma is thought to reflect regional connectivity in the service of current tasks. See Chapter 5.

ganglion (GAN-gee-on; Greek for ganglion ‘tumor on or near tendons’): A large cluster of **neurons**. The major subcortical organs may be considered to be ganglia, such as the **basal ganglia**. They are often very large structures, and have multiple functions. They are typically composed of subdivisions, which themselves are often layered and folded arrays of nerve cells. See Chapter 4.

gestalt (gesh-TALT; German for form): 1. A perceptual stimulus that cannot be reduced to simple subcomponents. 2. A branch of psychology based on the German concept of *Gestalt*, often summed up with the slogan that “The whole is more than the sum of its parts.” Gestalt psychology has profoundly influenced the study of perception. See Chapter 6.

glial cell (GLEE-el SEL; from Greek *glia*—glue): Non-neuronal cells in the brain that support neurons, maintain neurochemical homeostasis, form protective **myelin sheath** around neurons, and process information. See Chapter 14.

gray matter The outer layers of the **cerebral cortex**, as seen with the naked eye. Gray matter contains the cell bodies of tens of billions of **neurons** that send white-covered **axons** in many directions below the cortical mantle. See **white matter**. See Chapter 4.

Hebbian learning (HEB-ee-en LUR-ning): According to Donald O. Hebb, “neurons that fire together, wire together.” That is, two neurons strengthen their **synaptic** links if they are active at the same moment. This process forms **cell assemblies**. Introduced by Donald Hebb in 1949, it is also called Hebb’s rule. See Chapter 3.

Helmoltz, Hermann von (1821–1894): German physician, physicist, and sensory scientist. His works on vision and audition are still read, but his best-known contribution was demonstrating the physical law of conservation of energy using electrical stimulation of dissected frog legs. Helmholtz was one of the first to propose that the visual system makes “unconscious inferences” that go beyond the raw light input to the eyes, a controversial idea in his time that has become widely accepted. See Chapter 1.

hemispheric lateralization (hem-is-FEER-ik lat-er-al-ih-ZAY-shun; from Greek *he-mi-* (half) + *sphair-ion*—sphere; and Latin *lateralis*—side): The degree to which certain brain functions are performed primarily by one **cerebral** hemisphere, the most prominent being speech production on the left side for most people. See Chapters 9, 10, and 11.

hemodynamics (HEE-mo-dye-NAM-ics; from Greek *hema*—blood; *dynamos*—force or power): The study of blood flow changes, particularly in the brain, as an index of local neural activity. See Chapters 1 and 5.

hippocampus (hip-o-KAM-pes; Greek seahorse, from *hippos*—horse, *kampos*—sea monster): In the human brain, the hippocampi are looped structures in each of the two **medial temporal lobes**. The hippocampi are part of the **limbic system** and play basic roles in encoding and retrieving **episodic** and **semantic memories** and in spatial navigation. See Chapters 2 and 9.

homunculus (ho-MUN-cue-lus; Latin—little man): The distorted human body maps in the **primary somatosensory cortex** (the sensory homunculus) and in the **primary motor cortex** (the motor homunculus). The lips, hands, feet, and sex organs have more sensory neurons than other parts of the body, so the homunculus has correspondingly distorted large lips, hands, feet, and genitals. Each hemisphere contains a sensory and motor homunculus of the opposite side of the body. These body maps were discovered by neurosurgeon Wilder Penfield at the University of Montreal in the 1950s and 1960s. See Chapter 4.

hypothalamus (hie-po-THAL-a-mus; from Latin *hypo*—below; Greek *thalamos*—chamber): The major neuroendocrine organ of each side the brain, with vital roles in the regulation of blood nutrients, motivation, appetite control, and other major life functions. The hypothalamus is located below each **thalamus** just above the **brainstem**. It is closely related to the **pituitary** and **pineal glands**. See Chapter 4.

immediate memory (ih-MEE-dee-et MEM-er-ee): Also called short-term **memory**. The ability to recall something for 10 to 30 seconds without rehearsal. **Working memory** and **sensory memories** can be seen as specific kinds of immediate memory. See Chapter 2.

implicit memory (im-PLI-sit MEM-er-ee; from Latin *implicitus*—obscure): Unconscious **memory**, which may arise from conscious or unconscious events. See Chapters 2 and 9.

inattentional blindness (in-uh-TEN-shun-el BLIND-ness): A reliable experimental phenomenon in which one is not able to see things that are normally clearly visible. See Chapter 8.

inference (IN-fer-ens): Drawing a conclusion based on knowledge rather than direct observation. See Chapter 1.

inferior (in-FEER-ee-er; from Latin *inferus*—lower): Below. See Chapters 1 and 4.

insula (IN-soo-la; Latin for island): A structure that is hidden in and underneath the **lateral sulcus**, covered up by the **temporal** and **parietal lobes**, and therefore appears as an island when the covering tissues are gently pulled away. The insula is involved in “gut feelings,” such as the sense of nausea and disgust,

- and possibly in emotional feelings and cravings. See Chapter 4.
- intentionality** (in-ten-shen-AL-ih-tee): The “aboutness” of mental events, their ability to represent aspects of the world. Distinguished from *intention* as a mental goal. See Chapter 13.
- interaural level difference** (in-ter-OR-el; from Latin *inter*—between; *auris*—ear): A method of sound localization in which the brain detects the small difference in loudness between the two ears that occurs when a sound travels toward the head from an angle. See Chapter 7.
- interaural-time-difference** (in-ter-OR-el): A method of sound localization in which the brain detects the split-second delay between the time when sound from a lateral source reaches the near ear and when it reaches the far ear. See Chapter 7.
- intonation contour** (in-toh-NAY-shun kon-TOOR): The “melody” or singsong of normal speech. In English and other languages, questions typically are given a different intonation contour (a rising tone) compared with affirmative statements (a falling tone). See Chapter 11.
- ipsilateral** (IP-si-LAT-er-al; from Latin *ipse*—self; *latus*—side): On the same side of the body. See **contralateral**. See Chapters 2 and 4.
- James, William** (1842–1910): American psychologist and philosopher. James summarized the nineteenth century’s studies of the human mind and brain. His *Briefer Psychology* (1893) was widely used as an introductory text in psychology well into the 1920s. James also influenced Western stream of consciousness literature, educational psychology, and the study of religious experience and mysticism. In philosophy he is considered a major exponent of pragmatism, and was a source for European phenomenology. He was the brother of novelist Henry James and of diarist Alice James. See Chapter 1.
- lateral** (LAT-er-al; from Latin *lateralis*—side): On the side(s) of the brain. See Chapter 1.
- lateral geniculate nucleus** (LGN; LAT-er-el jen-IK-yoo-let NOO-klee-us; from Latin *latus*—side; *genu*—knee-shaped; Latin *nux*—nut): A nucleus consisting of “knee-shaped” layers of cells in the thalamus. It is the primary relay center between the retina of the eye and the **primary visual cortex** (Area V1). See Chapter 6.
- lateral inhibition** (LAT-er-el in-hi-BI-shun; from Latin *latus*—side; Latin *inhibitus*—restrain): The capacity of a **neuron** to reduce the activity of its neighboring cells in the same layer of neurons. See Chapter 3.
- lateral occipital complex** (LOC; LAT-er-el ox-SIP-ital KOM-pleks; from Latin *latus*—side; Latin *occiput*—rearmost part of the skull): A region on the side of the **occipital lobe** that has a general role in visual object recognition. See Chapter 6.
- lateral sulcus** (LAT-er-al SUL-cus; from Latin *latus*—side; *sulcus*—groove): Also called Sylvian fissure or lateral fissure. This prominent “valley” divides the **temporal lobe** from the **frontal** and **parietal lobes**. See Chapter 1.
- lexical identification** (LEKS-ih-kul eye-den-tih-fih-KAY-shun; from Greek *lexis*—word): The process of assigning words to speech sounds. See Chapter 11.
- lexicon** (LEKS-ih-con; from Greek *lexis*—word): The vocabulary of a language. See Chapter 11.
- limbic system** (LIM-bik sis-tem; from Latin *limbus*—border): A set of brain structures involved in emotion, memory, olfaction, and action control, including the **hippocampus**, **amygdala**, **thalamus**, **hypothalamus**, and **cingulate gyrus**. The limbic system is interwoven with the endocrine system and **autonomic nervous system**. See Chapter 13.
- long-term depression** (LTD; LONG TERM de-PRE-shun; from Latin *deprimere*—to press down): A lasting decrease in the strength of a **synapse**. Along with **long-term potentiation** (LTP), LTD is thought to be a synaptic basis for **learning** and long-term **memory**. See Chapter 3.
- long-term potentiation** (LTP; LONG TERM puh-ten-shee-AY-shun; from Latin *potentia*—power): A long-lasting strengthening of a synaptic link. Along with LTD, LTP is thought to be the synaptic basis of **learning** and long-term **memory**. See Chapter 3.
- longitudinal fissure** (lon-gi-TOOD-in-al FISH-er; from Latin *fissus*—crack, opening): The deep valley that divides the right and left hemispheres of the vertebrate brain. See Chapter 1.
- magnetic resonance imaging** (MRI; mag-NET-ik REZ-nence IH-ma-jing; Latin *resonare*—to sound; *imago*—imitation): Based on the spin resonance of atomic nuclei, MRI is a technique used to visualize the internal structures of the body, including the brain. **Functional MRI** (fMRI) records brain activity and is often superimposed on the structural brain image obtained via MRI. See Chapter 5.
- magnetoencephalography** (MEG; mag-NET-o-en-sef-eh-LOG-gra-fee; Greek *en-* + *kephale*—in the head; *graphein*—writing): An imaging technique based on the magnetic fields produced by brain activity. MEG is silent and noninvasive and has good temporal and spatial resolution. See Chapter 5.
- medial** (MEE-dee-al): Toward the midline of the body or the brain. **midsagittal**. See Chapter 1.
- medial temporal lobe** (MTL; MEE-dee-el TEM-per-el LOBE): The bottom aspect of the **temporal lobes**,

- which are arranged symmetrically around the midline, and contain evolutionarily ancient olfactory structures, memory encoding and recall, and emotional functions. See Chapters 2 and 4.
- memory** (MEM-ree, MEM-eh-ree; from Latin *memor*—mindful): A lasting brain representation that is reflected in thinking, experience, or behavior. See Chapter 9.
- mental flexibility** (MEN-tel fleks-ih-BIL-ih-tee; from Latin *mens*—mind; Latin *flexus*—bent; Latin *-ibilis*, from *-bilis*—capable or worthy of): Also called ability to shift **cognitive set**. The capacity to respond rapidly to unanticipated environmental contingencies. See Chapter 12.
- mentalize** (MEN-tel-ize; from Latin *mens*—mind): The ability to understand the self and others, not just as sensory objects but also as subjective beings with mental states. See Chapter 13.
- metacognition** (MET-a-cog-NI-shen; from Greek *meta*—above; Latin *cognere*—to know): Knowing about cognition **awareness and understanding of one's own thought processes**. See Chapter 8.
- midsagittal** (mid-SAJ-i-tal; from Latin *sagitta*—arrow): **medial**. The midline plane of section, going from the nose to the middle of the back of the head. In the brain, a midsagittal view shows a single hemisphere with a view of the brainstem, the corpus callosum, and the four lobes. See Chapter 1.
- mind** (from Greek *menos*—spirit): Those aspects of intellect and **consciousness** manifested in thought, perception, **memory**, emotion, will, and imagination, including all of the brain's conscious and unconscious cognitive processes. See Chapter 1.
- morpheme** (MOR-feem; from Greek *morphe*—form): The smallest linguistic unit that can convey meaningful information by itself. In English, prefixes and suffixes are considered to be morphemes (e.g., “pre-” and “post-”) as well as the single phoneme /s/, which can signify the plural. See Chapter 11.
- motion blindness** (MO-shun BLIND-nes): A symptom caused by injury to brain regions needed for motion perception, such as **area MT** of the visual cortex, resulting in an inability to perceive visual motion. See Chapter 6.
- multistable perception** (MUL-tee-STAY-bel per-SEP-shun) from Latin *stabilis*, from the base of *stare* ‘to stand’. Alternating visual perceptions of an ambiguous stimulus. See bistable perception and Chapter 6.
- myelin** (MY-e-lin; from Latin *myel*—marrow): A sheath of glial cells, called the myelin sheath, surrounding the **axons** of many **neurons**. Myelinated axons appear **white**, hence the “**white matter**” of the visible brain. See Chapters 1 and 3.
- neocortex** (NEE-o-COR-tex; from Latin *neo*—new; Greek *cort*—bark): The largest and most visible part of the human cerebral cortex. It is the “new” cortex from an evolutionary point of view, as contrasted with the “old” cortex of the **medial temporal lobe**, **hippocampus**, and olfactory brain. See Chapters 1 and 4.
- neon color spreading** (NEE-on CAW-ler SPRED-ing): A perceptual illusion in which white space appears to be tinted by proximity to colored and black lines. See Chapter 6.
- Neural Darwinism** (NUR-el DAR-win-izm; from Greek *neuron*—nerve): A theory proposed by physician and neuroscientist Gerald Edelman that suggests that neurons develop and make connections following Darwinian principles. In biological evolution, species adapt by reproduction, mutations leading to diverse forms, and selection among the resulting repertoire of slightly different organisms. Neural Darwinism suggests that brains develop in similar fashion, both in the reproduction, variation, and selection of developing neurons, and in a later stage, in the Darwinian selection of synaptic connections. Brains are said to be *selectionist* rather than *instructionist*, unlike the program of a digital computer. See Chapter 3.
- neural migration** (NUR-el my-GRAY-shun; from Greek *neuron*—nerve): Movement of nerve cells from their place of origin toward their final location in the developing brain. See Chapter 14.
- neural net model** (NUR-el NET MO-del; from Greek *neuron*—nerve): Also known as **artificial neural nets (ANNs)**, neural models are simulated, simplified models of selected brain functions. Most are relatively small in scale and do not represent the great complexity of the brain. However, they are important for a better understanding of how neural computation might work. See Chapter 3.
- neuromodulator** (NOOR-o-MOD-u-lay-ter; from Greek *neuron*—nerve; *modulate* is used in the sense of “influence” or “regulate”): Certain neurochemicals have very widespread effects in large regions of the brain. These are called **neuromodulators**, whereas **neurotransmitters** are molecules with very local effects in specific synapses. See Chapter 1.
- neuron** (NOOR-on or NYOO-ron; from Greek *neuron*—nerve): Nerve cells that transmit information by electrochemical signaling. They are the core components of the human brain, spinal cord, and peripheral nerves. Many different types of neurons exist, from sensory receptors and motor units and neuroendocrine cells to pyramidal neurons, which have long-distance axons; interneurons, which form bushy local connections; and a wide variety of specialized cells. See Chapter 3.

- neuron doctrine** (NOOR-on or NYOO-ron DOK-trin; from Greek *neuron*—nerve; *doctor*—teacher): The central theory of the neuron doctrine was a theory credited to the Spanish histologist **Santiago Ramón y Cajal**, stating that “the nervous system consists of numerous nerve units (**neurons**), anatomically and genetically independent.” This has been one of the basic assumptions of brain science for the past century. However, the discovery of large numbers of electrical synapses (gap junctions) may challenge some aspects of the neuron doctrine. See Chapter 1.
- neuropeptide** (NOOR-o-PEP-tide; from Greek *neuron*—nerve; Latin *peptidia*—small digestibles): A peptide is a short amino acid chain. Neuropeptides act as local neurotransmitters or neurohormones, influencing appetite regulation, growth hormone, and pain perception. See Chapters 1 and 3.
- neurotransmission** (NOOT-oh-trans-MISH-en): Electrochemical signaling between nerve cells. See Chapter 3.
- neurotransmitter** (NOOR-o-TRANS-mit-er; from Greek *neuron*—nerve; Latin *trans*—moving through): Chemicals that act to relay a signal from one neuron to the next across a synaptic cleft. Some neurotransmitters are packaged into **vesicles** that cluster beneath the membrane on the presynaptic side of a **synapse** and are released into the **synaptic cleft**, where they bind to receptors located on the postsynaptic membrane. Release of neurotransmitters often is driven by **action potentials** in the presynaptic axon. There is a low level of baseline release even in the absence of an action potential. See Chapters 1 and 3.
- object permanence** (OB-jekt PER-ma-nens): The knowledge that perceptual objects continue to exist even when they cannot be seen or touched. Object permanence begins in infants around 7 months. See Chapter 14.
- occipital lobe** (ox-SIP-it-al lowb; from Latin *occiput*—a back bone of the skull): The occipital lobes, which contain the earliest visual region of the cortex, are the smallest of four lobes in the human **cerebral cortex**. See Chapters 1 and 4.
- orbitofrontal cortex** (or-bit-oh-FRON-tel COR-teks; from Latin *orbis*—circle, orb, orbit, world: referring to the part of the brain immediately above the sockets or *orbits* of the two eyes).
- output functions** (OWT-put FUNK-shuns): Brain processes controlled by the **frontal lobes** that include the **central executive**, action planning, and motor output. See Chapter 2.
- paleocortex** (PAY-lee-o-COR-teks; from Greek *paleo*—old, ancient; Greek *cortex*—bark): An evolutionary ancient region of the **cerebral cortex** including the **medial temporal lobes**, olfactory cortex, and **hippocampus**. See Chapter 2.
- parahippocampal place area** (PAIR-a-HIP-o-KAMP-el (PPA); from Greek *para*—before; see **hippocampus** (PPA)): A region near the hippocampus that responds more strongly to landscapes and visual scenes than to isolated objects like houses or faces. See Chapter 6.
- paralinguistic** (PAIR-uh-lin-GWIS-tik; from Greek from *para*—near; Latin *lingua*—language): The non-verbal aspects of linguistic communication, such as voice intonation, gesture, social distance, and eye contact. See Chapter 11.
- parietal lobe** (puh-REYE-uh-tl lowb; from Latin *parietalis*—relating to walls): A large cortical region located above the **occipital lobe** and behind the **frontal lobe**. The parietal lobe integrates sensory information from different modalities, and contains constantly updated maps of the position of the body and nearby objects. See Chapters 1 and 4.
- Pavlov, Ivan Petrovich** (1849–1936): Russian physiologist. He was awarded the Nobel Prize in Physiology or Medicine in 1904 for research pertaining to the digestive system. He is best known for describing “classical conditioning,” in which an arbitrary stimulus like the sound of a bell came to signal the coming of a biological stimulus like food, thereby eliciting salivation. Pavlov’s proposal that conditional reflexes are the basic unit of all human **learning** is no longer generally believed. However, Pavlovian conditioning is widely used in research and is relevant to clinical issues such as food preferences and aversions, and perhaps anxiety disorders. See Chapter 1.
- Penfield, Wilder** (1891–1976): A neurosurgeon and researcher in Montreal who performed pioneering work in epileptic surgery. Before operating, he performed exploratory brain stimulation in awake patients (who were free of pain using only local anesthetic in the surgical opening). Thus patients could report their experiences upon electrical brain stimulation. Penfield and coworkers were able to determine functions of the human brain that were previously only approachable via post-mortem studies of brain damaged patients. See Chapter 5.
- perceptual filling in** (per-SEP-choo-el FIL-ing in): A general feature of sensory perception in which the brain fills in missing parts of a visual object or scene, often far beyond the direct sensory input. See Chapter 6.
- perceptual memory** (per-SEP-choo-el MEM-ree, MEM-eh-ree; from Latin *memor*—mindful): Long-lasting changes in one’s ability to perceive the world—for example, the ability to perceive the sounds of speech,

and to recognize visual objects under changes in orientation and lighting. See Chapter 2.

peripheral nervous system (PNS; per-IF-er-el NUHR-vus SIS-tem): The extensive network of neurons outside of the brain and spinal cord. The PNS includes sensorimotor neurons below the neck and autonomic neurons that innervate the smooth musculature of the digestive tract, heart, and circulatory system. See Chapter 4.

perseveration (per-sev-er-AY-shun; from Latin *perseverare*—persist): A symptom involving the inappropriate and uncontrollable repetition of a specific word, phrase, or gesture. See Chapter 10.

phoneme (FO-neem; from Greek *phōˈneː*—sound): In human languages, the smallest lexically distinctive category of sound, such as consonants and vowels. See Chapter 7.

pituitary gland (pi-TOO-uh-tehree gland; from Latin *pituita*—phlegm, from the former belief that the pituitary secreted phlegm): The “master gland” of the body, also called the hypophysis. An endocrine gland about the size of a pea that appears to hang from the **hypothalamus** at the base of the brain. The pituitary works with the hypothalamus to regulate developmental stages and homeostasis. See Chapter 4.

planum temporale (PLAH-num tem-por-AHL-eh; from Latin *planum*—a flat surface; Latin *temporalis*—of the temple): A part of the **auditory cortex** involved in sound analysis and particularly speech perception. Recently, the posterior portion of the planum temporale has been implicated in sensorimotor processing. See Chapter 7.

plasticity (plas-TI-SI-tee; from Greek *plastikos*, from *plassein*—to mold, form): The ability of the brain to adapt and reorganize to new environmental inputs or demands or following brain damage. See Chapter 7.

pons (PONZ; Latin, *pons*—bridge): A prominent anterior bulge in the **brainstem**. The pons relays sensory information between the **cerebellum** and the forebrain and spinal cord, helps to control sleep and wakefulness, and regulates respiration among other functions. It also generates **REM sleep** signals that are interpreted by the cortex as visually vivid, narrative dreams. See Chapter 4.

positron emission tomography (PET; POH-zi-tron ee-MISH-en tom-OG-reh-fee; Latin *emittere*—to send out; Greek *tomos*—section; Greek *graphein*—writing): Positrons are positively charged subnuclear particles, typically produced by a particle accelerator. PET is a low-level radioactive imaging technique that allows the computational extraction of brain or body slice maps, from which a three-dimensional image can be constructed. Typically, PET reflects metabolic activity. See Chapter 5.

postcentral gyrus (post-SEN-tral JEYE-res; from Latin *post*—behind; Latin *gyrus*—ridge): A protruding fold in the **parietal lobe** of the human brain immediately behind the **central sulcus**. It includes the **primary somatosensory cortex**, the first cortical map of the body senses, also called the **sensory homunculus**, which represents the opposite or **contralateral** side of the body. See Chapter 4.

posterior (pos-TEER-ee-er; from Latin *post*—after): Behind. In brain anatomy, **posterior** is synonymous with **caudal**.

prefrontal cortex (pree-FRON-tal KOR-teks; from Latin *prae*—in front of; *frons*—the forehead; Greek *cort*—bark): The large, forward portion of the **frontal lobes**, not including the motor cortex. Prefrontal cortex includes **executive** functions and Broca’s area, and is sometimes called “the organ of civilization.” See Chapters 2 and 12.

primary motor cortex (PRIE-mar-ee MO-ter KOR-teks; from Latin *primus*—first; Greek *cort*—bark): The brain region that directly controls skeletal (voluntary) muscles. It corresponds to the **motor homunculus**, and works in close association with other sensory body and motor maps, such as the premotor cortex. See Chapters 2 and 4.

primary somatosensory cortex (PRIE-mar-ee so-MAT-o-SENS-ery KOR-tex; from Latin *primus*—first, most important; *soma*—body; *sensus*—sense; Greek *cort*—bark): The sensory homunculus (body map), located on the **postcentral gyrus** of the cortex, it is the first cortical area for the body senses of touch, pressure, and pain. See Chapters 2 and 4.

primary visual cortex (PRIE-mar-ee VIZH-oo-el KOR-teks; from Latin *primus*—first, most important; Latin *visus*—sight; Greek *cort*—bark) (also called V1): The first cortical map of the visual system, located within the calcarine sulcus in the **occipital lobe**. See Chapter 6.

problem space (PROB-lem SPAYS): A graph of the decision points in problem solving, often in the form of a tree structure. See Chapter 10.

procedural memory (pruh-SEE-der-el MEM-ree, MEM-eh-ree; from Latin *procedere*—a way of doing things; Latin *memor*—mindful): A form of **implicit memory** equivalent to skill memory (such as riding a bicycle) or knowing how to do a task. It appears to be largely unconscious. This type of **memory** is often very durable. See Chapters 2 and 9.

radial unit model (RAY-dee-el YOO-nit MAH-del): A model of **neural migration** proposed by neuroscientist **Pasko Rakic** that asserts that in the developing cerebral cortex, the cells are created at the base of each cortical column and each new cell migrates past its predecessors. See Chapter 14.

Rakic, Pasko (b. 1933) (rah-KEECH): A neuroanatomist who showed that neural migration occurs radially as

well as rostrally, like the outflowing spokes of a forward-moving wheel. See Chapter 14.

Ramón y Cajal, Santiago (1852–1934): Spanish pioneer in microscopic studies of the brain. He often is considered to be the founder of brain science. Many of his detailed drawings of brain tissue slices are still presented today. See Chapter 1.

receptive field (ree-SEP-tiv FEELD; from Latin *recipere*—to take): The receptive field of a nerve cell in the visual system, for example, is the region of the visual field that can activate or inhibit the firing of the cell. The receptive field of a retinal receptor is therefore different from the receptive field of a higher level cell tuned to detect motion or visual object identity. Analogous receptive fields have been found for visual attention in the parietal lobe. Receptive fields are found in other sensory systems as well, such as the auditory and somatosensory systems. See Chapter 3, and see Chapter 6 for more discussion on receptive fields in the visual system.

reentrant connectivity (ree-EN-trent con-ec-TIV-e-tee): Most brain connections are bidirectional, in that activity at point A triggers activity at point B and vice versa. See Chapter 3.

reentry (ree-entry): In Neural Darwinism, the resonant looping between two neurons or arrays of neurons so that neuron A activates neuron B and vice versa. Reentry can also take place between neuronal populations. It is believed to be the primary signaling mechanism among brain regions and therefore closely related to brain rhythms. See Chapter 3.

reflex circuit (REE-fleks SIR-kut): Also called a reflex arc, this is the relatively simple pathway that mediates a reflex action. The most common example is the knee-jerk (or patellar tendon) spinal reflex, which occurs even when the spinal cord is isolated from the brain. However, spinal reflexes can be quite fast, complex, and coordinated, and may interact with the brainstem and the vestibular (balance) system, as in the case of a cat reorienting its body during a fall. Normally reflexes work in close coordination with voluntary control via the frontal lobes, cerebellum, and basal ganglia. Cranial reflexes like the pupillary reflex are under the joint control of autonomic, visual, and emotional regions of the brain. See Chapter 3.

region of interest (ROI; REE-gen of IN-trest): A region of the brain selected to be tested in a brain imaging study, in order to make statistically valid predictions about expected activity in that region. See Chapter 5.

reticular formation (reh-TIC-u-ler for-MAY-shun; from Latin *reticulum*—network): A part of the brainstem that is involved in the sleep-waking cycle and many

other functions. It receives collateral input from all sensory and motor systems, as well as from higher-level brain structures. It is evolutionarily one of the oldest parts of the brain. See Chapter 4.

retina (REH-tin-a): The array of light receptors lining the inner surface of the eye. Light striking retinal receptors (rods or cones) trigger a chemical reaction that evokes a change in electrical potential across the cell membrane. This may trigger activity in retinal ganglion cells that project their axons to make up the optic nerve, which terminates in the visual relay nucleus of the thalamus. See Chapter 6.

retrograde amnesia (RET-ro-grayd am-NEE-zhuh; from Latin *retrogradus*—going back; Greek *a-mne-sia*—without memory): A form of memory loss extending before the time of brain injury. Contrasted with **anterograde amnesia**. See Chapter 9.

sagittal (SAJ-i-tal; from Latin *sagitta*—arrow): Any section of the brain that runs parallel to the **medial** or **midline** cut. See Chapters 1 and 4.

selectionism (suh-LEK-shun-izm): A brain theory based on Neural Darwinism. In biological evolution species adapt by reproduction, mutations leading to diverse forms, and selection among the resulting repertoire of slightly different organisms. Neural Darwinism suggests a similar selectionist process in the growth of neurons and their synaptic connections. See Chapter 3.

selective attention (suh-LEC-tiv a-TEN-shun): The ability to pay attention to one aspect of the environment while ignoring competing stimuli. This may occur voluntarily, as in choosing to read an interesting book while sitting on a noisy bus, or when one sensory experience is biologically or personally significant. See Chapters 2 and 8.

semantic memory (seh-MAN-tic MEM-ree or MEM-er-ee): A type of **declarative memory** that involves meanings, factual beliefs, categories, and other general knowledge going beyond specific experiences. See Chapters 2 and 9.

semantics (seh-MAN-tiks): The study of meaning in language. See Chapter 11.

sensory system (SEN-suh-ree SIS-tem): Part of the nervous system responsible for processing sensory information (the primary five senses being visual, auditory, tactile, taste, and olfaction (smell)). A sensory system consists of sensory receptors, neural pathways, and mostly posterior cortex involved in sensory perception. The classical senses have many subsenses, like pain and even tickle sensations, light receptors in the eye that trigger melatonin as a sleep hormone, the balance sense, and the like. Not all sensory systems yield conscious experiences; blood

pressure, for example, which is sensed by hypothalamic neurons, is rarely conscious. The classical senses begin with receptor surfaces containing many millions of receptors, such as the retina and the basilar membrane. See Chapter 2.

sequential grouping (seh-KWEN-shul GROOP-ing):

One way in which the human auditory system organizes sound into perceptually meaningful elements. If sound properties are repeated in the same sequence, they may be grouped together. For example, the sound properties of your friend's voice may help you hear him speak in a noisy environment. See Chapter 7.

shadowing (SHA-doe-ing): An experimental technique to study selective attention in which subjects repeat speech immediately after hearing it. With practice, subjects can learn to shadow speech with a lag time of less than a second. The shadowing task is sufficiently demanding that other streams of speech cannot be understood at the same time. See Chapter 8.

simultaneous grouping (SEYE-mul-TAY-nee-us GROOP-ing) Latin *simul* 'at the same time': If two sounds have common onsets (beginnings) and offsets (endings), they may be grouped together. One way in which the human auditory system organizes sound into meaningful elements. See Chapter 7.

sound localization (SOUND lo-cal-ih-ZAY-shun): Identifying the location of a sound, often based on **binocular disparities** of timing and loudness between the two ears. See interaural level difference, interaural time difference, and Chapter 7.

source memory (SORS MEM-ree or MEM-er-ee): **Memory** for the specific time, place, and circumstances when an event was experienced. For example, you may remember not only when you learned about the theory of gravity (the memory), but also who first told you about it (the source). See Chapter 9.

spiking code (SPI-king CODE): The rate and pattern of action potentials, which may transmit useful information in the brain. See Chapter 3.

stimulus-driven attention (STIM-u-lus DRI-vn a-TEN-shun): The capture of **attention** by salient stimuli—such as the sudden honking of a car horn or the crash of a glass breaking. See Chapter 8.

Stroop test (STROOP test): Named after American psychologist John Ridley Stroop, who first wrote about this phenomenon in English in 1935. When the name of a color, such as *blue*, *green*, or *red*, is printed in a color differing from that expressed by the word's meaning (e.g., the word *red* is printed in blue ink), a subject has more difficulty naming the color of the word and is slower and more prone to errors than when the meaning of the word is congruent with its

color. This phenomenon is known as the Stroop effect. In order to correctly name the color of the ink (e.g., 'red') rather than the word (e.g., 'green'), the subject has to suppress the near automatic reading response in order to respond 'red'. Variations of the Stroop task have been used to investigate many aspects of automatic processing. The Stroop effect is useful in activating conflict-related regions of the brain, and generalizes well to related tasks, like the "emotional Stroop." See Chapter 8.

superior (soo-PEER-ee-er): Latin *superior*, comparative of *superus* 'that is above,' from *super* 'above.' Above. In the human brain, it is synonymous with **dorsal**.

supratemporal plane (SOO-pra-tem-per-el PLANE): A flat region of **cortex** in the Sylvian fissure, where primary and secondary auditory cortex and parts of **Wernicke's area** are located. See Chapters 4 and 7.

Sylvian fissure (SIL-vee-en FISH-er): Also called the **lateral sulcus** or lateral fissure. This prominent "valley" of the cortex divides the **frontal lobe** and parietal lobe above from the **temporal lobe** below. See Chapter 4.

synapse (SIN-aps): Synapses are tiny gaps between neurons that communicate by way of chemical neurotransmitters. Synapses are a basic computational element of the brain, a kind of traffic control point for the flow of information. The brain has tens of billions of neurons, but it has many trillions of synapses. See Chapter 3.

synaptic cleft (sin-AP-tic CLEFT): The space between two **neurons** that can communicate with each other via neurotransmitters. See Chapter 3.

synaptic pruning (sin-AP-tik PROO-ning): The selective loss of **synapses** in the brain when some potential connections are not utilized. See **Hebbian learning**, **neural Darwinism**. See Chapter 14.

synaptogenesis (sin-AP-toe-GEN-eh-sis): The birth of **synapses** in the brain. See Chapter 14.

syntactic analysis (sin-TAK-tik uh-NAL-ih-sus): The identification of grammatical structures from words, phonemes, and morphemes. See Chapter 11.

syntax (sin-TAKS): The rules and regularities of sentences in natural languages. See Chapter 11.

Talairach coordinates (tal-AY-rahk co-ORE-din-etz): A precise three-dimensional coordinate system for the human brain that can localize any point in the brain with millimeter precision. See Chapter 4.

temporal lobe (TEM-por-al lobe) from Latin *temporalis*, from *tempus*, *tempor-* 'time.': The temporal lobes are parts of the cerebral **cortex** that are involved in visual perception, hearing and speech perception, and **memory encoding** and **recall**. They emerge from the sides of the cortex, beneath the **lateral sulcus**.

- In profile, if the human brain resembles a boxing glove, the temporal lobes would be the thumb of each side. The temporal lobe envelops the **hippocampus** and **amygdala** and is therefore involved in emotion and memory formation as well. The **medial temporal lobe** (most easily seen from the bottom perspective of the brain) is ancient paleocortex, including olfactory cortex. See Chapters 1 and 4.
- teratogen** (ter-AT-e-jen): A chemical or other factor (such as prescription or non-prescription drugs or cigarette smoke) that causes developmental malformations. See Chapter 14.
- terminal** (TER-mi-nul): The distal end of an **axon**. See Chapter 3.
- thalamo-cortical system** (THAL-a-mo COR-ti-kel SIS-tem; from Greek *thalamos*—chamber; Greek *cort*—bark): A central hub in the brain involving the **cortex** and **thalamus**, allowing signal traffic to flow flexibly back and forth in both directions. See Chapter 4.
- thalamus** (THAL-a-mus; from Greek *thalamos*—room, chamber): A pair of symmetric egg-shaped structures in the brain that provide the main cortical input hub and cortico-cortical traffic hub. Plural: thalami. See Chapters 1 and 4.
- theory of mind** (THEE-eh-ree or THIR-ee of MIND): The ability to attribute mental states—beliefs, desires, intentions—to others. See Chapter 13.
- transcranial magnetic stimulation** (TMS; trans-CRAY-nee-el mag-NET-ic stim-yoo-LAY-shun): A relatively noninvasive method using powerful electromagnets outside of the head to stimulate or inhibit cortical neurons. TMS shows good temporal and spatial resolution. See Chapter 5.
- unconscious perception** (un-CON-shus per-SEP-shun) From Latin *un* (not) + *conscius* ‘*knowing with others or in*’: Sensory stimulus processing without awareness of the stimulus—such as the sudden honing of a car horn or the crash of a glass breaking. See Chapter 6.
- ventral** (VEN-trel; from Latin *venter*—the belly): The lower part of a brain structure, inferior.
- ventricles** (VEN-trik-lz): Four small cavities in the brain containing circulating cerebrospinal fluid. The ventricular walls have been found to be sites for neural stem cells. See Chapter 4.
- ventromedial prefrontal cortex** (ven-tro-MEE-dee-el pree-FRON-tal KOR-teks; Latin *venter*—the belly; *medialis*—in the middle): The bottom midline structures of the frontal lobe, especially in humans and other primates. This region, extending backward from the top of the nose, is involved in emotions, infant-mother bonding, fear, and risk in decision making. See Chapter 12.
- verbal rehearsal** (VER-bel ree-HER-sel): Mental repetition of words to be remembered, using the “inner speech” component of *working memory*. Inner speech involves a spontaneous commentary on current concerns, goals, and emotions. See Chapter 2.
- Vesalius, Andreas** (1514–1564): Belgian physician who produced the first accurate atlas of human anatomy in 1543, called *On the Fabric of the Human Body*. Vesalius’ book was a major milestone in the Renaissance rediscovery of science and medicine. See Chapter 1.
- vesicle** (VES-i-cl; from Latin *vesicula*—small bladder): The small bubbles filled with neurotransmitter molecules that travel through the axon to the synaptic terminals, where they fuse with the synaptic membrane to release neuromolecules into the cleft when an action potential occurs. Neurotransmitters then diffuse across the synapse to trigger depolarization of the postsynaptic membrane, ultimately leading to another axonal spike. Vesicles are essential for the propagation of signals between neurons and are constantly recreated by the cell. See Chapter 3.
- visual agnosia** (VI-zhoo-el ag-NO-zhe; from Greek *agno-sia*—lacking knowledge): A condition in which a person has difficulty recognizing objects because of damage to object-recognition regions of the cortex, such as the inferior temporal lobe. See Chapter 6.
- visual backward masking** (VI-zhoo-el BAK-werd MAS-king): A conscious visual image can be “erased” by a subsequent visual event, such as a cross-hatch display, even though the conscious event is not physically blocked from reaching the retina. See Chapter 8.
- visuospatial sketchpad** (vizz-oo-oh-SPAY-shul SKECH-pad): The ability to hold visual and spatial information momentarily in **working memory**. See Chapter 2.
- volition** (vuh-LI-shun) From Latin *volitio(n-)*, from *volo* ‘*I wish*’: Voluntary control of actions, as contrasted with automatic control, as in the case of highly practiced habits. Many brain disorders involve a loss of voluntary control. See Chapter 12.
- Wearing, Clive** (b. 1938): A prominent British classical musician who suffered a viral brain infection in his forties that destroyed both hippocampi and some frontal lobe regions. Wearing’s case has become well known due to the efforts of his wife, Deborah Wearing, to raise public awareness of such medical conditions. Wearing lives in a single, blindered moment, without the ability to store information for later recall. Despite his **memory** problems, he is still able to play the piano and conduct musical pieces he

knew well before the brain injury. See **anterograde amnesia**. See Chapter 2.

Wernicke, Carl (1848–1905): German physician and discoverer of a selective cortical region for speech comprehension. This region is now referred to as **Wernicke’s area**, and the associated deficit is known as **Wernicke’s** or **receptive aphasia**. Patients with this deficit cannot understand speech, including their own, but produce fluent-sounding (but not usually meaningful) speech. See Chapter 1.

Wernicke’s aphasia (WER-nik-ees AY-PHAY-zha; from *a*—without; Latin *phasia*—utterance): See **Wernicke, Carl**. See Chapter 1.

Wernicke’s area (WER-nik-ees AIR-ee-a): An area of the upper posterior temporal lobe that is needed

for language comprehension. See Chapters 1, 7, and 11.

white matter: In the brain white matter consists of dense bundles of myelinated **axons**, which connect various **gray matter** areas of the brain to each other. White matter is named for the appearance or massive numbers of **myelinated** nerve axons, which appear to form the visible core of brain structure. See Chapter 1.

working memory (WUR-king MEM-ree or MEM-er-ee): A cognitive capacity for storing and manipulating novel information over 10 to 30 seconds. Working memory includes **central executive**, **working storage**, **verbal rehearsal**, and the **visuospatial sketchpad**. See Chapter 2.

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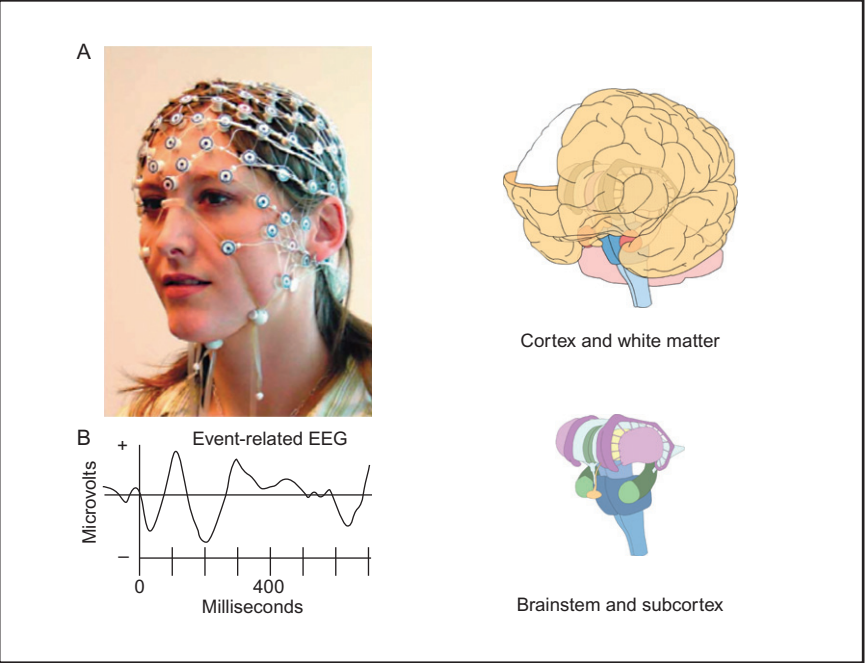


PLATE 1 A first approach to the anatomy of the brain. **A.** Always keep in mind how the brain is situated in the human head. It's the first step in appreciating the spatial layout of the cortex, which is filled with some 85% white matter, the shielded 'highways' that link all the major regions to each other. *Bottom right:* The cortex is mounted on the brainstem and subcortex, which flows up from the spinal cord. The event-related EEG is a reminder that the young lady in **A** has a constant, dynamic flow of massive signal traffic flowing through her brain, which we can pick up with surface EEG.

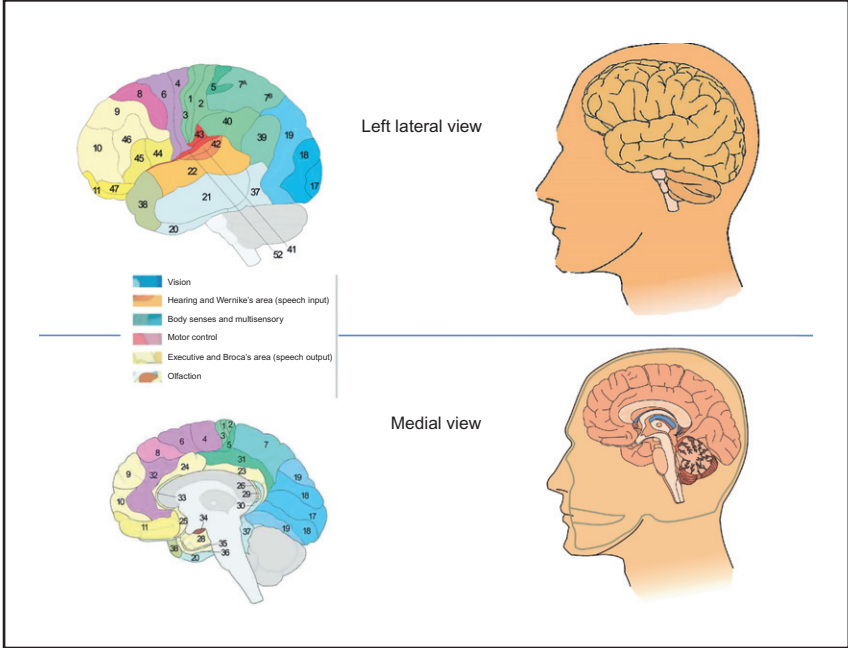


PLATE 3 The specialized regions of the cortex, the huge covering of the brain. Cortex is a flat sheet that is folded into the upper cranium. Notice the colored regions – the major functions of the cortex. It is the cortex that is believed to support the specific contents of conscious experiences. Its posterior half is sensory, its front half is motor and 'future directed' – cognition, working memory, planning, decision-making.

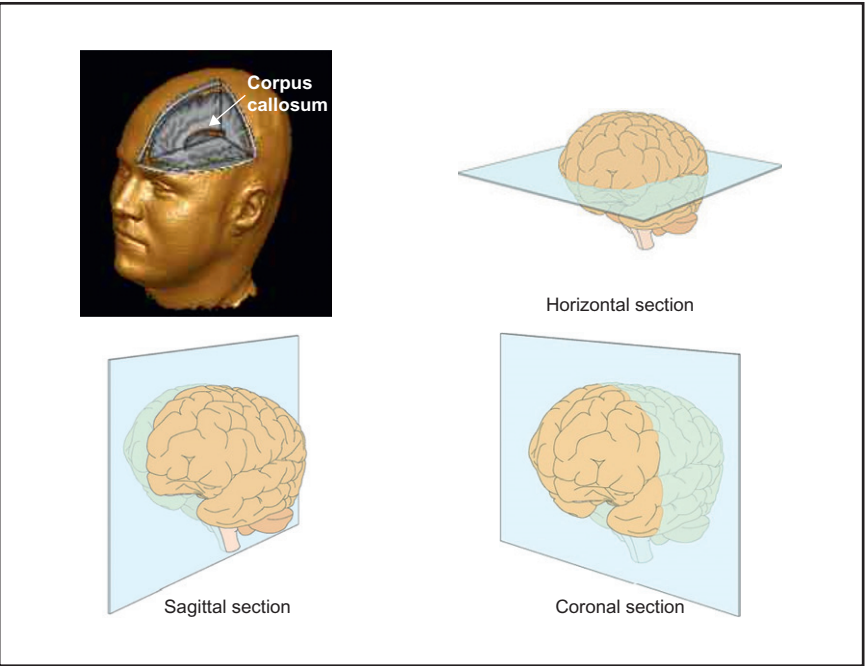


PLATE 2 Use the human head (upper left) to stay oriented. We can see the corpus callosum from the left side. The brain has three major planes of section to keep in mind.

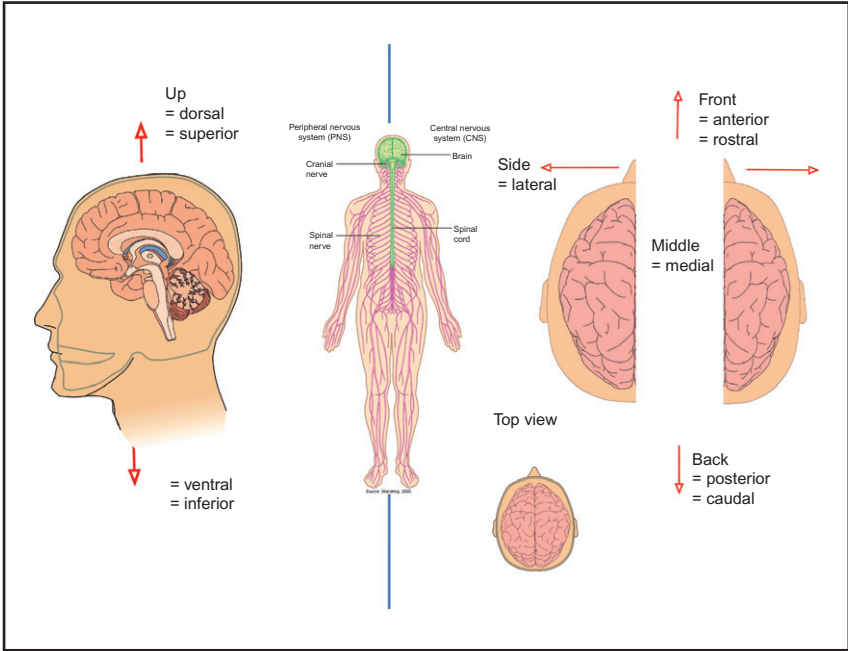


PLATE 4 Neurons pervade the body, and the spinal cord is a great highway channel between the brain and the rest of the body. Left, we see the brain from a left medial perspective. Notice the canonical directions, which are like North, South, East and West in geography. The simplest terms are given on top (Up, Down, etc.). But anatomists always use the Latin-based words. Use this figure for reference if you need to understand a brain figure in the book.

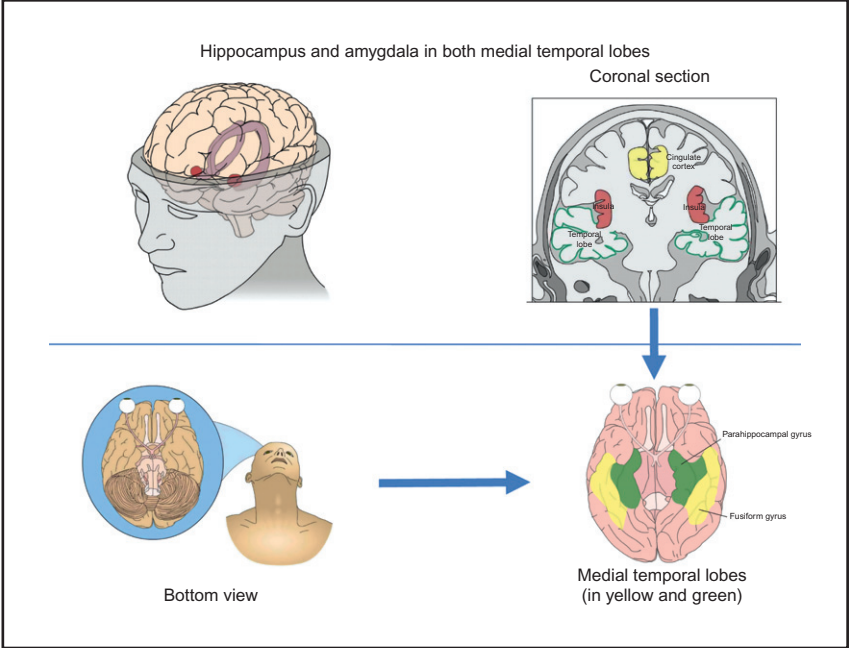


PLATE 5 Again, begin with the human head, and notice how the two hippocampi are nestled inside of each of the two temporal lobes. A vertical slice from ear to ear (coronal) only shows the hippocampi as small circular disks (red). On the bottom, if you imagine craning the head backward, you can visualize the location of the medial temporal lobe (MTL) which contains the two hippocampi. Those structures are crucial for emotion, vision, and memory.

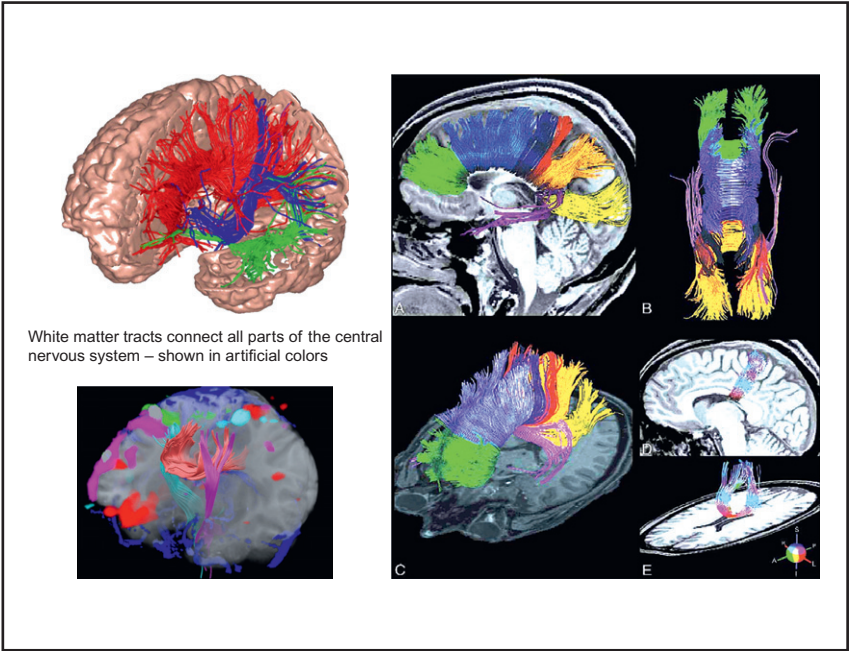


PLATE 6 Upper Left: The white matter tracts emerge in a great ‘fountain’ of fiber tracts from the thalamus. Other fiber tracts run in all the major directions. Below and to the right are *tractographs*, specialized MRI scans that show the massive highways between all major parts of the brain. Almost all are bi-directional. Source: Upper left, Izhikevich & Edelman, 2008; right side: Hofer & Frahm, 2006.

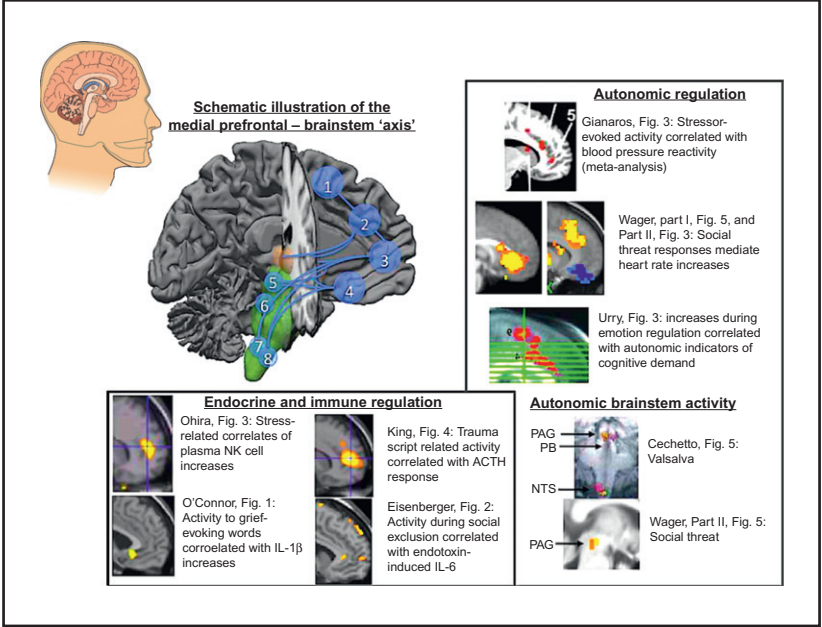


PLATE 7 The body and brain are highly interconnected. Upper left, we see how the medial view of the brain (facing right) is well-connected with endocrine system (hormonal) and immune regulation, and with autonomic regulation (heart, lungs, stomach, intestines, and blood vessels). Humans have no voluntary control over these functions, unlike our external muscles of the body and head. Source: Lane & Wager, 2009.

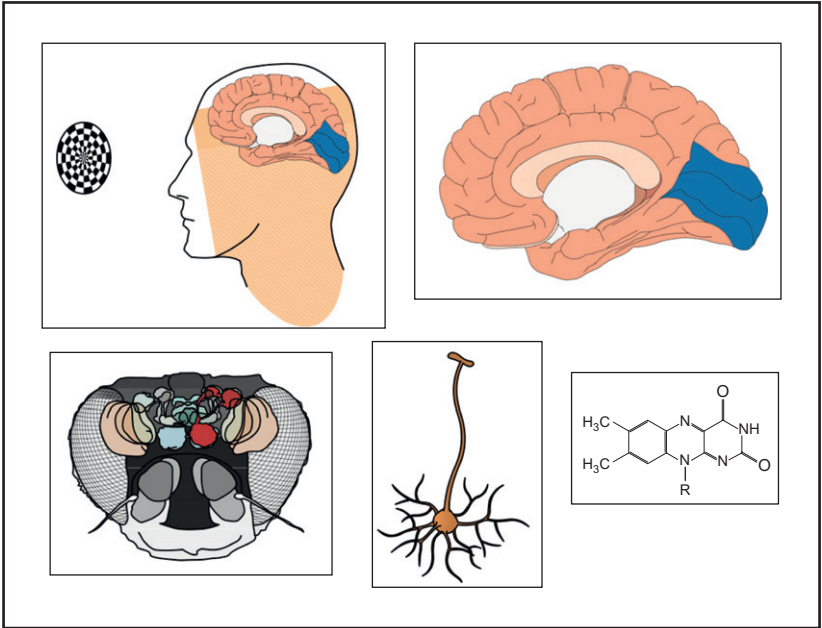


PLATE 8 A wider perspective. On the upper left, we see a person looking at a rotating visual disk, which triggers widespread brain activity, beginning in area V1 (dark blue). V1 is as big as a credit card, but it is folded inside the occipital lobe. Below, we see a comparison to a fruit fly brain, which has perhaps 100,000 neurons. A single neuron is shown to the right, followed by a single organic molecule, an amino acid (because of the amine fraction (NH), and a carboxyl fraction (COOH)). All the vertices in the diagram stand for carbon atoms. R refers to a side chain, which could be quite variable. All levels of analysis, from molecules to gross anatomy, are vitally important. All proteins and many neurotransmitters involve amino acids.